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Phytosociology of the bottomland hardwood forests in western Montana

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PHYTOSOCIOLOGY OF THE BOTTOMLAND HARDWOOD FORESTS

IN WESTERN MONTANA

By

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INTRODUCTION

The forests that prevail in the bottomlands of western Montana are described by Kirkwood (1922). He states, "the broad-leaved, deciduous element in the forests ... is seldom conspicuous, but along open river bottoms, *Populus trichocarpa* is everywhere the dominant tree, sixty feet in height, three feet or over in diameter, and sometimes with a clear, cylindrical trunk of forty feet in length" (p. 135). Two other types of lowland forest, those occurring along valley tributary streams, and those inhabiting lake shore edges, possess a similar appearance because of the dominance of *P. trichocarpa*.

The sites along the main rivers and those along lake shores and tributaries have certain characteristics in common. In all of these areas where *P. trichocarpa* is the dominant tree, the water level is close to the surface. However, there are certain environmental characteristics which differ in the main river sites and those along lake shores and tributary edges. Perhaps the most important difference is that the communities away from the main river channels are normally not subject to the degrees of disturbance created by the annual river floods.

Because of the proximity to other more coniferous forest types, the physical position of these cottonwood forests often lend themselves to different floristic features. This was particularly evident when comparing cottonwood communities found along major rivers to those found in the narrower tributary valleys which were surrounded by the coniferous montane forests.

The cottonwood stands in the narrower tributaries are often in close approximation to the coniferous forests occurring on the mountain slopes and may possess many species in common with the adjacent forests. As the narrow ravines widen at greater distances from the mountain forests in the direction of the larger river courses, the abundance of many of these coniferous forest species decreases in the flora, and the more characteristic species of open valley floodplain communities dominated by black cottonwood become more common.

A quantitative description of black cottonwood communities in western Montana is lacking, and since these are a conspicuous part of the forests of western Montana, this description would be of interest. One community has been described by Habeck (1963) in a discussion of the climax forests in the Lake McDonald region of Glacier Park. However, as Kirkwood (1922) states, the cottonwood forests are widespread in the bottomlands and, as will be demonstrated, the composition given by Habeck for the single stand does not demonstrate the variability that can be found when examining other sites where P. trichocarpa is growing.

Geographically Populus trichocarpa ranges from Alaska to southern California and northern Baja California, east to southwestern Alberta to western Montana, Idaho, western Wyoming, and western Utah (Hitchcock, et al., 1964). Balfour (1943) feels that at a given latitude black cottonwood has the greatest altitudinal range for any tree on the North American continent.

Roe (1958) in reviewing the literature of black cottonwood states that it grows in a variety of climatic and edaphic environments where temperatures range from 117°F to -53°F and for optimum growth, abundant soil moisture, nutrients, oxygen and high pH are needed (Smith, 1957). However, the range of tolerance is wide for *P. trichocarpa* (Roe, 1958).

It has been stated that detailed quantitative studies of this type are lacking for western Montana. Jeffrey (1964) has published a study dealing with forest types along the Liard River in Northwest Territories, in Canada, and Orloci (1963) has described some environmental factors affecting vegetational types on the Squamish River, in British Columbia. Studies in eastern North America have been more numerous. The Mississippi River and its tributaries have been the site of many of these phytosociological studies; Aikman (1948), Barclay (1924), Dietz (1950), Griswold (1942), Hosner (1960), Hosner and Minckler (1963), Lee (1945), Leopold (1941), Lindsey *et al*. (1961), Shelford (1954), Shull (1944), Ware (1955), and Yeager (1949). Other extensive studies include Buell and Westendahl (1955) on the Raritan River in New Jersey and Hefley (1937) on the Canadian River in Oklahoma.

It is evident from this partial comparison of studies done on bottomland communities in the northwest and those in other parts of the country, that there is a scarcity of knowledge and understanding of lowland forest communities in this western region.

It was the purpose of this investigation to study as wide a range of variation in bottomland forest plant composition as possible. A quantitative description of these communities was then made and an ordination was constructed by utilizing such measurements as tree density, frequency, and dominance; sapling density and frequency, and herb and shrub frequency. Soils were also collected and analyzed for a variety of nutrients, pH, and water holding capacity. Qualitative, descriptive observations were made of lowland forest successional patterns as well as on various river dynamics which influence bottomland vegetation behavior.

DESCRIPTION OF THE STUDY REGION

Location: The Continental Divide in Montana separates what is known to many as eastern and western Montana. The western portion of the state, except for the region northwest of the Cabinet Range, is drained by the Clark's Fork of the Columbia River. The Clark's Fork is fed from the north by the South, Middle, and North Forks of the Flathead River and the Blackfoot River, from the east by the upper Clark's Fork and from the south by the Bitterroot River (see Fig. 1).

The lowland forests in western Montana occur in three basic physiographic sites: along the bottomlands and floodplains of major rivers, along the edges of smaller valley streams and tributaries, and along lake and oxbow shores. Major river stands that were sampled in this study were located on the Clark's Fork of the Columbia, the Bitterroot, the Blackfoot, and the Middle and South Forks of the Flathead Rivers. Smaller tributary valley stands were located on Rattlesnake Creek in Missoula County, Sweeney and Bass Creek in Ravalli County, and Snyder Creek near McDonald Lake in Glacier National Park. Smaller lake stands were located at the edge of various oxbow lakes in the vicinity of Kalispell in Lake County (see Table 1).

The valleys in western Montana where black cottonwood is prevalent have been in the past, and are now, subject to alluviation from the surrounding mountains. The land forms which have resulted in the valleys from this sedimentation are a direct result of the types of rocks and the degrees of erosion from the surrounding mountain ranges. Correspondingly, the types of rocks found in the mountains and the manner of their formation might greatly affect the bottomland vegetation.

<u>Geological History of Western Montana</u>: The Rocky Mountains extend north and south across western North America and inland 500 to 1,000 miles. These western mountains are called the North American Cordillera or Cordilleran system. This name is derived from the Spanish word meaning "cord" or "rope." This is indicative of the appearance of the mountain chain. These mountains are remnants of upward folds and crumples of upheaved blocks in the earth's crust. They are younger than the eastern North American mountains, and this is partially evident by the difference in the degree of erosion which has taken place on the two groups (King, 1959). The western mountains are therefore much higher and often form barriers for plant migration. These may be physical barriers, or the mountains, valleys and streams may cause environmental conditions limiting the extension of plant ranges.

The Rocky Mountains vary in elevation and reach a peak of 14,495 ft. at Mt. Whitney in the Sierra Nevada. The Cordillera is formed by many of the mountain forming processes; volcanic activity, folding, faulting, uplift, and erosion. Some areas show evidences of tilting and these are in various locations altered by river erosion and ice action.

One author (Fenneman, 1931) points out that most mountains of the Cordillera are not arranged in lines, and often the term "range" is misleading because of the lack of definite borders between the mountain groups. Many neighboring groups of divides are on closely similar levels. Recent faulting, differences in rock structure and unequal erosional forces may cause slight differences in the peak heights. Fenneman (1931) refers to the portion of the Rockies in northern Idaho and western Montana as being similar to an approximate peneplain raised to a level from 6,000-9,000 ft. and dissected by age.

Many of the present topographical features of the Cordillera are results of the actions of the Tertiary and Quaternary times. Some areas, although they are basically of a different structure formed at a pre-Tertiary time, are covered by processes such as volcanic activity during the Tertiary.

King (1959) states that in Canada the portion of the Rockies closest to the Great Plains is composed of miogeosynclinal strata. These are mainly Paleozoic but with Triassic and Jurassic sediments above. The miogeosyncline area borders the more inland continental areas, and is approximated to the west by a eugeosyncline area. Miogeosynclines are deposits laid down in shallow water or low areas and like the eugeosynclines are areas of massive deposition and sedimentation. This area of miogeosyncline was subjected to slow sedimentation, little crustal activity and no volcanic activity. The exterior ranges west of the main Rocky Mountains consist of eugeosynclinal rocks similarly of Paleozoic, Triassic, and Jurassic age that have been deformed greatly and metamorphosed and plutonized, or formed by solidification of a molten magma deep in the earth (Webster, 1961). The orogeny or uplift of the mountains was earlier on this eugeosynclinal side nearest the Pacific Ocean, and the miogeosynclinal region arose later. The first orogeny occurred during the latter half of the Mesozoic and the miogeosynclinal one a little later.

If a survey is made of the Cordillera south of the Canadian border, the mountain origin becomes more complex. Up to this point, it has been stated that the Rockies begin with the miogeosyncline, the eastern edge being composed of Paleozoic rocks; the pre-Cambrian rocks are wedged at the base. But this miogeosyncline lies on the western edge of the Colorado Plateau. East of this line of miogeosyncline is what is known as the Eastern Ranges and Plateaus.

The Northern Rocky Mountains which extend from western Montana into Canada are ridges of sedimentary rocks originating in the miogeosyncline belt of the Cordillera. These have developed a folded and faulted nature. Between the north and south ranges of the Rockies are those that extend northward into southern Montana and Idaho. On the west, these are deformed miogeosynclinal rocks and to the east of these are those ranges which formed from simple uplifts outside of the main miogeosynclinal belt.

During the Paleozoic era, the miogeosyncline was undergoing great sedimentary action with little interruption and under shallow depth of water. Sediments formed readily here at this time. In the miogeosyncline in western North America the portion toward the continent was marked by a thinning of the sedimentary section. A segment of the miogeosyncline from west central Montana across the border into Canada exhibits a wide surface extent known now as the Belt Series.

The Belt Series makes up much of the northern Rocky Mountain rock formation. These are formations of sandstone, shale, and limestone with the limestone forming a small part of this. In many places the sandstone is changed to quartzite and in most of the series the shale is changed to argillite which is a hard slaty shale. This is gray, dull green or red. These rock formations were first studied in detail by C. D. Walcott in the Big and Little Belt Mountains near Helena, Montana and are therefore known as the Belt Series.

The Big and Little Belt Mountains are part of the eastern ranges of the Cordillera and these mountains lie near the edge of the sedimentary basins. To the east, the Belt Series protrudes out between basement and Paleozoic rocks. This series forms most of the Rocky Mountains in northwest Montana, northern Idaho, southwestern Alberta, and southeastern British Columbia. The thickness of the Belt Series increases to the west from about 13,000 ft. near the Belt Mountains to 45,000 ft. in the Purcell Mountains (King, 1959; p. 133). The Belt Series exhibits only a few limestone reefs as indications of early life, and these, it is believed, were produced by lime secreting algae. Most of the Belt Series are sedimentary, but Purcell lava occurs in some ranges.

In northwestern Montana the younger deposits of the miogeosyncline which lie above the Belt Series are only seen in infrequent exposures, because much of these have been eroded away and deposited into the valleys. Thus, it can be pointed out that it is difficult to determine the extent of the later sediments, except it is believed the extent of these younger sediments was similar to that of the Belt Series. The Belt Series disappears beneath younger layers in the mountains north of the border.

The main direction of mountains and valleys of the Cordillera is interrupted between Helena and Missoula in the east, and in the Spokane area in the west. The result is that in this region, the valleys assume a west-northwest direction (King, 1959; p. 140). These valleys are believed to be local discontinuous high angle faults. North and south of this line, called the transverse zone, the valleys run in north-northwest direction and are the result of folds, block thrusts or low angle thrusts.

The Bitterroot Valley which drains into the Clark Fork River from the south is bordered on the west by the Bitterroot Range and on the east by the Sapphire Range. The Bitterroot range is the eastern portion of the larger Idaho mountain mass (Ross, 1950) (see Fig. 1). The altitude of the range increases gradually in a southerly direction to the highest point of the range, Trapper's Peak at 10,175 ft. The effects of alpine glaciation are prominent in the cirques, the ravine walls, and marshes in U-shaped valleys at the heads of the canyons that extend down the east slope of the mountains (Kirkwood, 1922).

The east slope of the Bitterroot Mountains indicates a faulting (Pardee, 1950; Lindgren, 1904) and a rearranging due to the pressures of the arising Idaho Batholith. The granite that is present in the Bitterroot Mountains is part of the Idaho Batholith which forms most of the mountains of central Idaho. It is believed by some that this had its orogeny during the Nevadan orogeny, but did not become a part of the Bitterroots until the Laramide orogeny when masses of granite were left in the region south of highway 10 (King, 1959; p. 141). Following the faulting came a long period of erosion of the higher sediments which resulted in the exposure of the granite and the deposition of the eroded sediments into the valley of the Bitterroot. This erosion resulted in a moderate relief of the mountains. Lindgren (1904) states that a second uplift raised this eroded surface again to several thousand feet. He feels this was of post Triassic and pre-Miocene times. However, some feel this last faulting was of an earlier time (Ross, 1950). Breaks along the present western margin of the plateau at the foot of the fault resulted in the formation of the Bitterroot River.

Campbell (1916) and McMurtrey et al. (1959) both point out that the Bitterroot Valley is a structural trough which is the result of the faults at the base of the Bitterroot Mountains on the west and the Sapphire Mountains on the east side of the valley. The block strata was then depressed between these faults.

The Bitterroot River at present cuts through various levels of terraces in the valley leaving broad floodplains in many portions. The Bitterroot Valley is composed of a great quantity of Tertiary sediments derived from the highlands. In an area near Corvallis, bedrock was not reached at a depth of 1,450 feet. Quarternary deposits consisting of glacio-fluvial, glacio-lacustrine and talus deposits mantle the upper terraces and Tertiary and Quarternary deposits on the east side of the valley mantle the higher terraces there. The lower terraces in the valley consist of gravel, silt and sand of various sortings (McMurtrey, et al., 1959).

The glaciation of the Bitterroot Mountains during the Pleistocene resulted in deposits of glacial debris on the west side of the valley, and finer stream deposits accumulated at the foot of the non-glaciated Sapphire Mountains to the east. Water flowing out of these two mountain ranges varies markedly in its chemical nature. The dissolved salt concentrations coming from streams flowing out of the Sapphire Mountains, composed primarily of sedimentary Belt rocks, is considerably higher than the concentration of salts found in the water of the tributaries flowing out of the Bitterroot Mountains which are composed primarily of igneous rocks (M.C. McMurtrey, et al., 1959).

The Missoula Valley (Pardee, 1950) is about 8.5 miles wide in the vicinity of Missoula, and trends in a northwesterly direction for about 30 miles. The elevation of the valley is about 3,200 feet (see Fig. 1). It is drained by the Clark's Fork of the Columbia which enters the valley from the east and flows west to the region where the Bitterroot River joins it and then flows along the base of a series of sheer rock outcrops on the west side of the valley. The river in the Missoula Valley is composed of wide floodplains, oxbows and low swales until it flows through a deep gorge near Alberton, Montana.

Konizeski et al. (1965) state that the Missoula Valley can be described by four basic topographical units: the Clark's Fork floodplain, low terraces, and higher terraces. These higher terraces in the north-east portion of the valley slope upward to a deeply dissected northside ridge, parallel to the valley wall. Smaller, isolated terraces occur locally in the valley at different levels. Many erosional scars and oxbows in the low fringing terraces mark the old pathways of the river. These terraces are as much as 2 miles wide in the region of Missoula (Konizeski, et al., 1965). These may be separated from the floodplain by 20 foot scarps. Higher terraces reach a width of four miles in the central valley of Missoula. These slope gradually toward the mountains to a maximum elevation of about 3,250 feet. This flat ridge extends the length of the valley and is dissected by the six major tributaries which feed the Clark's Fork from the northeast. These tributaries in some cases, such as the Rattlesnake Creek, are narrow, flat valleys showing evidences of stream meandering and terraces (Nelson and Dobell, 1961).

The Missoula Valley is filled with deposits of Tertiary, Oligocene or Miocene age (Nelson and Dobell, 1961). The basin during this time was gradually depressed and deposition continued over the Pre-Cambian sedimentary rocks. Erosional deposits from the peneplain (Pardee, 1950; p. 366) to the east of the valley and from the surrounding hills filled the valley with possibly 13,000 feet of detritus (Konizeski et al., 1965). The deposits accumulated forming floodplains, ponds, marshlands and alluvial outwashes in the form of fans. These deposits of shale and conglomerates were later covered by a few hundred feet of channel gravel and sand of Pliocene age. Later earth movements during late Pliocene tilted this Tertiary strata to the northeast. During the Pleistocene with the formation of Glacial Lake Missoula, the Missoula and Bitterroot valleys were flooded and drained during various glacial and interglacial periods. The result was deposition of more than 200 feet of glacio-lacustrine gravel, sand and clay. The Clark's Fork River and its tributaries are now cutting into these Pleistocene deposits as well as more recent deposits (Konizeski, et al., 1965).

The Mission, Swan and Flathead Ranges run approximately north and south and divide that portion of western Montana into Mission, Swan and South Fork Valleys. The Blackfoot Valley, inclined in a more southwesterly direction, drains the southern end of the Swan Valley and mountains (see Fig. 1).

These valleys are composed of erosional debris from the surrounding mountains which are composed mainly of rocks in the Belt Series. Pleistocene and recent alluvium is present along the floodplains, but a thorough investigation has not been made in these areas to show the extent of fill in the various valleys or the degree of deposition preceding the advance of Pleistocene glaciation. The glaciation left its mark here as it did in many other areas of western Montana and many U-shaped tributary valleys of the region are the result. Numerous morrainal deposits in the Blackfoot Valley near Ovando, Montana, also appear to have come from local glaciers originating in the surrounding mountains. Numerous kettleholes in this region are the result of these glaciers.

Glaciation: Glaciation in western Montana during the Wisconsin and pre-Wisconsin stages of the Pleistocene left many remnants. Some of these are seen in the oxbow lakes and kettleholes in the upper Flathead Valley and Blackfoot Valley, shallow lakes in the Swan Valley, large terminal moraines in the Flathead Valley, and the lake deposits and shoreline formations in portions of the Clark's Fork tributary valleys.

During the Wisconsin stage of the Pleistocene, ice was continuous across North America from the Atlantic to the Pacific. The glaciers, however, are categorized into two main groups: the Cordilleran Glacier Complex which occupied the mountains of western North America and the Laurentide Ice Sheet which was spread from Newfoundland to the Rocky Mountains. The Cordilleran Glacier Complex during the Wisconsin centered in British Columbia and stretched northwest, and southwest mainly, but sent relatively small lobes down into northwestern Montana (Flint, 1947).

During the Wisconsin and pre-Wisconsin, a large glacier moved down the Kootenai River valley and across the present international boundary. In the location where the Kootenai River leaves the main Rocky Mountain Trench, this ice mass split. Some of it moved down the Rocky Mountain Trench, and another portion followed down the Kootenai. The portion moving down the Rocky Mountain Trench then continued and was joined by numerous local glaciers. These came from the North, Middle and South Forks of the Flathead River. These local glaciers pushed through what is now Bad Rock Canyon with a thickness that is estimated at about 3,000 ft. (Alden, 1953). Others came from the Whitefish Range. A glacier from the Swan Valley also joined this major tongue. This Swan glacier was apparently moving in a northerly direction and upon meeting the larger tongue it was turned back on the west side of the Mission Mountains to move also in a southerly direction with the larger glacier from the north. Grooves in the rocks in the lower end of the Missions were apparently left by these glaciers, and Alden (1953) points out that a moraine north of the gap through which the Swan River flows may be the terminal moraine of the Swan Valley Glacier.

Before the glaciation of the Flathead Valley and during the earlier Tertiary times, the outlet for Flathead Lake had been west of the Big Arm out the Big Draw and down the Valley of the Little Bitterroot. However, it is believed now (Alden, 1953) that pre-Wisconsin glaciation filled the Big Draw and closed this outlet.

During the Wisconsin Glaciation, the Flathead Glacier pushed down over what is now Flathead Lake, and it is believed to have left the terminal moraine or Polson moraine in the region just south of the present lake. It is thought by some that at the time of the formation of this moraine, Glacial Lake Missoula washed up against the south shore of this Polson moraine. With the formation of this moraine and with the formation of a terminal moraine in the valley of the Little Bitterroot, both from pre-Wisconsin and Wisconsin glaciation, Flathead Lake was hemmed in. The inter-glacial period resulted in the lake rising and glaciers receding. The water then began to flow over the Polson moraine in the region of the present outlet. At the time when this flowage began, the moraine was 3,200 ft. and at this time the water has cut to 2,885 ft. Much of this cutting was through relatively soft terrain, probably similar to that found throughout the valley, but the last 115 ft. was through Belt Rocks. The result of the lowering of the outlet was a lower lake level (Alden, 1953). The presence of Belt Rocks in this cut indicates the possibility that this Cambrian sedimentary material is the parent material underlying this valley.

When the glaciers receded in the region of Kalispell, the Flathead River, which had been flowing south from Bad Rock Canyon, moved west into its present course. This movement was across the old sedimentary lake bed. The glaciers in the Whitefish mountains also melted and the Flathead and its tributaries migrated laterally, meandering through the old lake bed. The present day indications of this migration and glacial melting lie in the swamps, kettleholes and oxbow lakes of this upper Flathead Valley region.

During the Wisconsin, the Purcell Trench which lies west of the Rocky Mountain Trench was occupied by a lobe of the Cordilleran Glacier. A portion of the glacier moved into the valley of the Clark's Fork east of Lake Pend Oreille to block the effluent of the Clark's Fork. The result of this was the formation of a large lake in the Clark's Fork Drainage. This lake was named Glacial Lake Missoula. It extended into the Bitterroot, upper and lower Clark's Fork, Blackfoot and Flathead Valleys (Beaty, 1962). One of the most evident features on the hillsides near Missoula is the shoreline formations, left by the Glacial Lake Missoula. These occur prominently in the valleys of Missoula, Ninemile, and the Bitterroot, and in parts of the Flathead and Jocko Valleys. Waters of this region have been noted at various depths. The greatest depth of the lake was in the region of Stevensville. Here beach lines are observed at 4,200 feet. This would place the depth of water about 1,000 ft. over the city of Missoula (Beaty, 1962; Campbell, 1916; Pardee, 1910).

The glaciers that came down from Canada were believed to have filled all of the mountain valleys in the north and filled them to depths of up to 1,000 ft. "Ice was more than 2,000 ft. thick on Lake Pend Oreille in Idaho" (Beaty, 1962; p. 113). The blockage of the northern valleys prevented outlet there.

Silt deposits which can be seen in various portions of the Lake extensions are found in basins adjacent to large ice masses or directly downstream from the larger ice masses. It is pointed out that the main valley floors of the Bitterroot and Clark's Fork east of Missoula lack deposits of silt, and this may be due to later stream action as well as lack of deliverance of the silt waters from the main lobes of the Cordilleran Glacier (Beaty, 1962).

<u>Soil Features and River Dynamics in Western Montana</u>: A consideration

of the soils in river bed areas has been made by workers in various parts of the country (Orloci, 1962; Jeffrey, 1964; Beaufait, 1955; Hosner and Minckler, 1960, and others). Several examples have been cited in the geological section dealing with the valleys in western Montana (McMurtrey, et al., 1959; Konizeski, et al., 1965; Beaty, 1962 and others). Many of these workers in other parts of the country and especially in western Montana feel that the main features of the present bottomlands were formed by alluvial deposits during past glacial or interglacial epochs. Major parts of alluvium may consist of material deposited on higher level floodplains, and then carried down by tributaries or the main river as it meanders across the higher floodplains and erodes to the lower levels.

In the forest stands studied, which were found on the larger, more open, active river floodplains, the more recent alluvium forms the major layer on which the herbaceous plants subsist. The soils consist of dispersed boulders interspersed by coarse graveliferous sand and finer sand. Finer silts, clay and fine organic debris are often found in aggregated distribution. Higher portions and less disturbed areas of the same island or stand may show development of a littler layer of organic debris derived from the surrounding vegetation. The soil types in the bottomlands are usually not homogeneous or continuous throughout the stands. Areas closest to the water are the most homogeneous because there usually is no vegetation which can cause leeward accumulation of silt and debris carried in the spring flood water. In cases where trees and shrubs are present, micro-edaphic habitats develop from the scattered deposits of clay, silt and organic debris.

Hosner and Minckler (1963), Lindsey, et al., (1961), Orloci (1963) and others all state that local deposits of fine silt may occur on the river systems that they studied in the midwestern and northwestern United States. This is also true in western Montana. There may be a small deposition of fine silt and clay, overlaid by deposits of sand. These local deposits of silt and clay may have developed from small floodplain lakes which form behind sandbars initiated by fallen trees, or the bole of a larger cottonwood. The bole would act to slow the water flow to a great extent and cause a precipitation of finer particles from the main stream flow. Leeward sides of fallen trees and depressions and backwaters in the floodplain stands which retain silt maintain their moisture through much of the summer and support quite a different flora than the drier, sandy sites which may have less water holding capacity.

In contrast, the tributary stands and oxbow stands are characterized by a more homogeneous soil type and a well developed litter layer is usually present. In the tributary stands this is underlain by coarse gravels and sand layers. The oxbow stands in the Flathead Valley were underlain mostly by a fine clay. These stands normally are characterized by the near absence of flooding and prolonged inundation.

It is evident that the soils of major river systems, and at times tributary stands, are subject to changes controlled by the frequency and degree of flooding, and the subsequent abrasive power of the flood. Lindsey, et al. (1961) state that flooding strength may vary depending on river cross section and bank height. Flooding may vary, depending on the stream with which one is dealing. Also, he states that "flood stage and any particular stage above it may be expected with decreasing frequency downstream" (p. 108). This he further explains would depend on the width and the height of the stream bank. The wide floodplains which are characteristic of the Tippecanoe River and the Wabash River (Lindsey, <u>et al</u>., 1961) would naturally hold more streamflow than those rivers that characterize western Montana which have a smaller floodplain and valley width. In the case of western Montana one would expect greater flooding further down the stream course because of the relatively smaller floodplains further down the river. In many instances rivers in western Montana may open into broad floodplains for many miles only to be constricted into a narrow gorge where the water cannot be withheld by broad floodplains typical of many midwestern rivers such as the Tippecanoe.

Erosion and deposition along river systems is greatly dependent on stream velocity. An interesting set of figures concerning stream strength is emphasized by Flint <u>et al</u>. (1941). They state that doubling stream velocity may increase stream abrasive power by four times, increase capacity to transport rocks of a given size by as much as 32 times, and increase the volume of the largest piece of rock the stream can push along its bed by as much as 64 times. Similarly, as has been stated earlier, reduced velocity may be correlated with the deposition of gravels, sand, silt, and clay as both the speed and level of the water decrease. Therefore, in receding flood waters, and also at normal stream level, in the still water of a convex bank of the stream bend, depositions occur and bars are built up. This may narrow the channel and cause the current to erode the opposite bank. Lateral stream migration then may result. As successive portions of the bar become emergent for a sufficient time during the growing season, Equisetum spp., and later Salix spp. and Populus trichocarpa may invade and stabilize this land form.

Within the river systems of western Montana the character of the deposits is related directly to the velocity of the water which has been carrying them. This varies according to the lateral direction of river migration, tributary inlet position and the nature of the soil through which the river travels. There are therefore numerous interacting forces which destroy any theoretical gradient of gravel in the upper courses, sand in the lower and silt in the lowest deltas. Trees, shrubs, rock ledges, slough depressions and wrecked car bodies are other factors affecting land deposition.

Portions of the main river channel that do not become dry until midsummer and fall often remain as coarse gravels and boulders with very little sand and silt mixed. This is probably due to the continued erosive power of the rivers and lack of silt remaining in the water when it finally recedes from this land. The gravel parts, due to the lack of water holding capacity, are usually devoid of vegetation with the exception of saplings, shrubs or clumps of grass-like plants which have been rafted there.

In a study made in the Northwest Territories, soils were described as having a high incidence of buried organic layers (Jeffrey, 1964). These are said to be the result of frequent deposition of sands above the organic layer. This is also common along the larger rivers in western Montana.

Table 2 demonstrates that in areas close to the main river system and in areas where flooding in the spring is common, the higher organic matter in the second layer is a frequent occurrence. Stands 10, 12, 13, 15, 18, 19, and 20 all show this character in the soils. It is interesting to note that although the majority of these stands do occur on the active floodplain, stands 18 and 19 are found on the shores of oxbow lakes in the Flathead Valley. These are subject to overflow in years of above normal high water like 1964. Apparently it is at this time that buried organic layers become a part of the soil profile even in these areas which appear to be removed from the overflow of the rivers. It is apparent from Table 2 that none of the tributaries have these buried soil layers. A deeper litter layer and higher per cent of organic matter is the most obvious difference in the soil types between the tributary stands and the active floodplain stands.

In some of the floodplain stands that are further removed from the flooding of the river viz. stands 8, 22, and 24, there is a higher per cent organic matter in the first layer than in the second. Although a larger sample would be needed to demonstrate this principle more conclusively, it is apparent that this may be due to two factors. First, these stands are less subject to flooding because of their greater distance from the main river system. Second, the coarser sand particles settle out of the water first because of their size and consequently stands like 10, 12, 13, and 20, which are located close to the active floodplain, have a higher per cent sand in the first soil layer than those stands like 8, 22, and 24 which are found further from the main river channel either in height or in linear distance. Therefore, even if the flood water does reach the stands further removed from the active floodplain, the waters would tend to be more laden with finer silts which are often higher in organic matter. The overall load carried by these rivers would be inversely proportional to the distance from the main channel. As the current is decreased more and more of the stream load is deposited. In areas where soils are composed of higher amounts of fine glacial clay, such as the Flathead Valley, viz. stands 18 and 19, the deposition of clays causes an inversion in the soil layers at relatively long distances from the main stream channel because of the small size of the clay particle, and its resultant property of being transported relatively long distances in the river load. In areas where these higher clay soils do not exist, clay deposition does not occur to as great an extent. The percent of inorganic particles that are carried longer distances is apparently not as great. The finer particles in these areas that are carried relatively long distances from the river systems are apparently composed of a higher per cent of organic matter.

One final but important point should be mentioned. These buried organic profiles often occur as extremely local depositions. For instance, often different parts of an island may show extreme differences in the soil depths. Earlier portions of the island contain deeper soils than those parts that support young stands of P. trichocarpa which presumably have become established later. Therefore, in the older portions of the island buried profiles may exist, and in those younger parts of the island, these may be absent. Instead these younger stands may be characterized by boulders overlaid by coarser sands. This is one of the earliest stages in the development of soils in the bottomlands.

Wind deposition also occurs on some rivers in the northwest (Jeffrey, 1964). This takes place in the winter when the winds are highest. Sand particles are transported mainly from exposed sand bars. Enhancing the effect of this phenomenon is probably the lower level of the water at this time. During the winter, and just before the spring runoff, water levels are probably lowest exposing more area to wind deposition. Jeffrey notes the bryophyte layer of surrounding areas to be covered with sand which could only have gotten there by wind deposits from exposed sand bars.

Lindsey et al. (1961) state that islands may develop by the river segmenting a portion of land previously continuous with the recent flood-plain. This might be the result of lateral migration and severe erosion. They state that the major cause for island formation in some rivers may be due to local sediment accumulation. The factors affecting sedimentation have already been enumerated. In western Montana both of these phenomena appear also to be major processes involved in island formation.

During the spring of 1964 damage from floods occurred. Table 3 compares the average peak stream flow for a year period with the peak of 1964. Extreme conditions of erosion were noted in all of the stands sampled. The combination of above average snowpack, and a sudden warm period of rain in early June caused these abnormal conditions of flooding. The most severely damaged were those stands on the South Fork of the Flathead where excessive erosion was most evident at the junction of the White River. Small creeks leading into tributaries of the South Fork such as Holbrook, Haun and Big Salmon creeks showed signs of extensive damage.

<u>Climatic Features</u>: Western Montana climate is influenced greatly by the Pacific Ocean. The Continental Divide (see Fig. 1) exerts a large influence on the climate of western Montana, preventing colder arctic air masses from entering western Montana. The western part of the state therefore has warmer winters, cooler summers, less wind, more cloudiness, a shorter growing season and more evenly distributed rainfall in comparison to the eastern part of the state. The mountains of the western part of the state receive a succession of air masses from the northwest, often times in rather rapid order, and this results in an instability of the climate during the months of September to June. These mountains also cause certain precipitation on their windward sides <u>viz</u>. Flathead County, Mineral County, Sanders County and parts of Glacier National Park. They consequently cause a rain shadow effect on their lee side. The Bitterroot Valley is one example. It obtains an average of 12.08 inches per year at Hamilton and 12.76 inches of rain in Missoula. Snow accumulation in the mountains of western Montana usually results in runoff and high river marks within the first two weeks of June (Anon., 1941). Rainfall is greatest in the months of May and June in western Montana.

In the bottomlands the snow accumulation and the runoff has a marked effect on those plants that grow below the high water line. Some authors (Orloci, 1963) feel this is the most important climatic factor influencing the vegetation on a river in British Columbia. This is naturally a direct result of the climate for the past few months, for the runoff is dependent on the climate. This also appears to be true for the areas in western Montana that were visited, for plants may be inundated late into June when the snow accumulation in the mountains has been heavy. It is for this reason that if a direct account was given of the months of heaviest precipitation and the effect this has on the whole upland flora in western Montana, this would not be completely applicable to those plants which grow below the high water mark along the major rivers. Many of the plants here lag behind those on drier sites due to the flooding by the rivers. It is therefore important to include in this section on climate not only data on precipitation and temperature, but also data on high water periods of some of the major rivers sampled. These data are not available for the minor creeks but they are available for the larger river systems of western Montana (see Tables 3 and 4). It is important to note that these peaks in high water were above normal and therefore the results of flooding that were noted in the stands during the summer of 1964 were not the results of an average year. Instead the effects that were seen in this summer of sampling were often severe erosion. This especially affected the understory plants, for in some places sedimentation and erosion eliminated them from the sample viz. stand 19.

The weather data that are given are those taken in towns near the stands that were sampled. This probably does not represent the exact condition that exists in the stands themselves, however, these are the only data that are available since with the wide geographic range of the study constant weather stations could not be maintained, and the data that could have been obtained in one visit would have been inadequate for a comparison of the different stands. This same problem occurs for obtaining micro-environmental data. These types of data would have been useful in the interpretation of the vegetation that occurs in the stands, but because of time, distances and the inaccessability of some of the areas these data were not obtained.

REVIEW OF LITERATURE

Floristic Uniqueness of Western Montana: Migration of plants and climatic changes may cause hereditary changes to occur in populations, and floras in a given region may become far more complex than if the climatic conditions had remained stable (Palomine, 1960).

It has already been illustrated that of all the areas that were sampled in the Bitterroot, Missoula, St. Regis, Blackfoot, Flathead, and McDonald valleys, only the Bitterroot and Missoula and St. Regis valleys were not glaciated during the Pleistocene and these were covered intermittently by many feet of water from glacial Lake Missoula. During glacial periods, with a lowering of temperatures and with an inundation of some areas by water and ice, some plants were able to migrate, and others were replaced by plants more resistant to cold. These survived only in isolated refugia.

"No fossil records are known which divulge the history of Idaho vegetation during the Pleistocene age" (Daubenmire, 1952; p. 14). This area of western Montana, especially in its northern part, might be considered comparable to northern Idaho in its Pleistocene vegetation, but again studies have not been made to indicate the Pleistocene vegetation of the area. Studies of pollen analysis in Idaho indicate that post-Pleistocene vegetation has not varied significantly except to demonstrate slight changes in elevation for the different forests (Daubenmire, 1952). This may also be true for western Montana, but the studies have not been made here to confirm this.

Various workers, (Benson, 1957; Daubenmire, 1952; Kirkwood, 1922;

Rydberg, 1915), have described the origins of the modern floras in western Montana and adjacent Idaho. These are by no means complete (Kirkwood, 1922) and the origins of many plants now present in western Montana are still to be determined. A comparison of plants encountered in this study to those plants discussed by other workers mentioned above is interesting.

Post-Pleistocene migration of floras in western Montana and their survival was determined by "climatic, topographic and edaphic conditions" (Kirkwood, 1922; p. 64). He lists three general regions as areas of origin from which the modern flora may have been derived: the north, presumably from the northern boreal forest; the east, presumably from the great plains; and the west or northwest. "As the western ... slope of the divide is the more favorable for the forest growth and is tenanted by a greater variety of species, it naturally follows that the western element is the most conspicuous in the forest flora of the Rocky Mountains ...." (Kirkwood, 1922; p. 67). He correlates this presence of the Pacific forest in western Montana with the favorable climatic conditions _viz_., greater rainfall, higher relative humidity, less severe winds, prevailing winds, varied habitats. He also states that many of the plants mentioned were derived from the Pacific flora and have wings for wind dispersal or are surrounded by fleshy fruits for dispersal by wildlife.

Table 5 illustrates the possible origins of the major dominants of trees, shrubs, and herbs in the stands that were sampled. It is apparent that the presence of the floristic elements is dependent upon geographic, climatic, and topographic position of the sites. Kirkwood

(1922) also states that these factors are important in determining forest distribution in western Montana. Table 1 illustrates the geographic location of the bottomland forest stands. Table 6 describes some of the climatic and topographic features of the communities.

Deschampsia caespitosa, Rhamnus alnifolia, Ribes hudsonianum, and Shepherdia argentea which are species of the northern forest are nearly restricted either to stands at high elevations or to stands occurring in cold air drainages at the mouths of mountain canyons. Juniper communis and Alnus incana, although they are quite widespread, reach their highest importance value in high altitude and tributary stands. This is particularly evident with J. communis. It reaches its highest importance values in stands 13 and 14. Both of these are at an elevation of about 4,660 feet, and at somewhat higher latitudes.

Chrysopsis villosa, the eastern plains representative, is found in disturbed floodplain stands at both high and low elevations. These stands, where this species is found, have a shallow organic layer, and the soils are generally coarser sands overlaying larger boulders. This is an extremely dry site except for the few weeks of inundation that occur during early June. z
western

The northern species, Abies grandis, Picea engelmanni, Rubus parviflorus, Sorbus scopulina, and Holodiscus discolor are mostly restricted to either higher elevations or narrower tributary valleys often in areas of suspected cold air drainage. Other species such as Amelanchier alnifolia, Crataegus douglasii, Philadelphus lewisii, Betula occidentalis, and Pseudotsuga menziesii have a much wider distribution. Those stands having the greatest number of Pacific forest species are the ravine and tributary stands where presumably moister atmospheric and edaphic conditions are present. It has already been mentioned that the more open floodplains are subjected to drying winds during most of the year, being located in the open valleys, and except for the inundation period, the soils are quite dry.

Geographic Distribution of Bottomland Forests: In the stands sampled, Populus trichocarpa was the most common tree dominant (see Tables 7, 8 and 9). This is true throughout the hardwood stands found on the active floodplain of rivers in western Montana. "P. trichocarpa is the most common of all trees along streams on the west slope of the Rockies in Montana and northern Idaho" (Kirkwood, 1922; p. 56). This is the only species of cottonwood found west of the Continental Divide in Montana (White, 1951). P. trichocarpa is probably "the most common cottonwood in western Montana; pioneers readily along roads, barrow pits, mine tailings, and other disturbed areas in its habitat" (Morris, et al., 1962; p. 41).

In western Montana the black cottonwood occurs in pure stands along major rivers as well as in mixed stands along major rivers, tributaries, large lakes, and oxbows (see Tables 7, 8 and 9). In the mixed stands it is associated with Picea engelmanni, Pinus contorta, Thuja plicata, Tsuga heterophylla, Abies grandis, Pseudotsuga menziesii, Populus tremuloides, Crataegus douglasii, Alnus incana, Betula occidentalis, Salix alba, Tsuga heterophylla, Pinus monticola, Larix occidentalis, Betula papyrifera, and Abies lasiocarpa.

Populus tremuloides achieves dominance in certain stands along rivers and oxbows in the valleys of western Montana (see Tables 7, 8 and 9). "It is not abundant in Montana but is of wide and frequent occurrence as individuals or small thickets ... throughout the state, notably in several localities about Missoula, along the Bitterroot, Blackfoot and Flathead Rivers ..." (Kirkwood, 1922; p. 53). Although P. tremuloides does reach dominant proportions in some stands along the Blackfoot and Bitterroot Rivers, it occurs more commonly on less disturbed upland sites, as exemplified by the oxbow stands in the Flathead Valley and in the region near Ovando, Montana. P. trichocarpa is more common along the principal river systems and floodplains than is P. tremuloides (see Table 8).

Community Composition of Bottomland Forests in the Northern Rocky Mountains: Lynch (1955) describes a Populetum-Asterosetum type in the aspen grovelands of Glacier County, Montana. He states that this association occurs along temporary streams and ponds in "inter-morrainal troughs or depressions" (p. 335). This type occupies the largest area of the grovelands. It is dominated by P. trichocarpa on the moister sites, and P. tremuloides on the drier sites. The most common understory plants of this type are Aster foliaceus var. parryi, Fragaria virginiana var. glauca, Elymus glaucus, Geranium richardsonii and Thalictrum occidentale. He states that Aster foliaceus var. parryi has the most indicator value declining in importance on both the wetter and drier sites. Lynch also states that in the same area in another association, the Populetum-Osmorhizetosum, both P. tremuloides and P. trichocarpa occur together. This association is found in the bottoms of "narrow mountain valleys formed by piedmont glaciers, from moist slopes near the mountains to the bottoms of intermorainal depressions" (p. 336). This is of fairly small extent and "specific in habitat" (p. 337). The characteristic understory of this association is *Osmorhiza occidentalis*, *Heracleum lantanum*, and *Viola canadensis*. He recognizes this association as distinct from the *Populetum-Asterosetum* because of the difference in characteristic species.

Lynch (1955) lists *Salix bebbiana*, *Cornus stolonifera*, *Rosa* spp., *Rubus idaeus* and *Lonicera involucrata* as common shrubs occurring with *P. trichocarpa*. The herb strata is characterized by *Calamagrostis canadensis*, *Aster ciliolatus*, *Rubus pubescens*, *Mertensia paniculata*, *Fragaria* spp., *Equisetum* spp., *Epilobium angustifolium*, *Thalictrum venulosum*, *Galium boreale*, *Vicia americana* and *Pyrola asarifolia*.

Moss (1953) describes the poplar associations occurring along river flats in northwestern Alberta. Although he is dealing with a different species of poplar, *Populus balsamifera*, it is of interest to note the apparent ecological similarity between the behavior of *P. balsamifera* and *P. trichocarpa* when they occur in stands containing *P. tremuloides*. When *P. balsamifera* is found growing with *P. tremuloides*, *P. balsamifera* is usually found in the moistest sites. This is similar to what Lynch (1955) has observed with *P. trichocarpa* and *P. tremuloides* associations, and what is generally apparent in western Montana.

Orloci (1963) was able to show a positive correlation between the vegetation and an environmental continuum on the Squamish River in British Columbia. He used the formula proposed by Major (1951), $v = f\ (cl, p, r, o, t)$, to describe environmental effects on the bottomland vegetation. This formula describes the vegetation as a product of the climate (cl), parent material (p), relief (r), organisms present (o) and time factor (t). Orloci modified this for application to the bottomlands by using V = f (Od, Sd, St, L, s, A). In this formula Orloci infers that the bottomland vegetation is primarily a product of the number of overflow days (Od). Orloci substitutes overflow days (Od) for climate. It has been stated that the climate which determines the snow accumulation during the winter and the spring runoff is of extreme importance to the bottomland flora in western Montana. Orloci substitutes soil depth (Sd) and soil texture (St) for parent material. He substitutes bench level (L) for relief. He retains organisms (o) in his formula, and substitutes aggradation or the "time which was needed to build up the bench level to its present position which is more or less equal with the age of the stand (A) which grows on it" (p. 35).

Orloci draws the following conclusions: higher bench levels yield greater soil depths, finer soil textures, and less frequent overflow. The age of river stands are proportional to the height of the benches with the higher benches supporting the oldest stands. Each plant species occurs in a certain bench level segment which is subject to definite amounts of overflow. The quality of the subsoil seems to have a more important effect than the topsoil. He demonstrates the use of environmental factors arranged in gradients and correlates these with a vegetational continuum. On the floodplain benches Scouleria aquatica and Hygrohypnum ochraceum are present where boulders are the soil texture and soil depth is zero. Where sand is underlain by gravel, and the soil depth is 7-14 inches, Equisetum arvense is present. With boulders partially covered by sand and soil less than fourteen inches, Salix sitchensis, Salix lasiandra, Alnus rubra, Populus trichocarpa and Scouleri *aquatica* are present. Where the soil depth is 14-27 inches and is composed of sand underlain by gravel *P. trichocarpa*, *Alnus rubra*, *Salix sitchensis*, *Salix lasiandra*, *Picea sitchensis*, *Lonicera involucrata*, *Rubus spectabilis*, *Elymus glaucus* and *Maianthemum dilatatum* are present. *Oenanthe sarmentosa* is present with the above group when "sand is underlain by a thin silt or clay horizon and gravel" (Orloci, 1963; p. 51). Where loam and silt are in the top horizon and sand and silt underlie these, *Picea sitchensis*, *Populus trichocarpa*, *Thuja plicata*, *Acer circinatum*, *Oplopanax horridus*, *Ribes bracteosum*, *Gymnocarpium dryopteris*, *Circaea alpina*, *Tiarella trifoliata*, and *Mnium insigne* are present. Loam and silt in the top horizons underlain by sand and gravel with the gravel close to the surface support *Picea sitchensis*, *Populus trichocarpa*, *Acer circinatum*, *Symphoricarpos rivularis*, *Disporum oreganum*, *Mnium punctatum*. The last two segments in the vegetational continuum have soil depths of greater than 27 inches. With the exception of the last two segments, in each successive segment there is a general decline in overflow days and an increase in the bench level height. The last two segments have the same number of overflow days and the same bench level height.

Jeffrey (1964) in a study of the forest types of the Liard River in the Northwest Territories states that *Picea glauca* is the most important forest tree in that area. It is a dominant in a wide range of soil and topographic sites in the lowland terraces and ancient floodplains. It is associated with *P. tremuloides*, *Betula papyrifera*, *P. balsamifera* and infrequently with *Picea mariana*. *Picea glauca* has its best development in the recent floodplain where it forms stands in mixtures with Populus balsamifera and Betula papyrifera. The seedlings of white spruce occur in the Balsam poplar - Equisetum pratense, Balsam poplar-white spruce - Equisetum pratense, white spruce-balsam poplar, white spruce-white birch forest and a mixed leaftree forest dominated by white birch, with trembling aspen as a co-dominant.

Taxonomic Problems: There were a number of problems that arose in the identification of the specimens obtained in the bottomland stands. The first and most difficult problem concerned the phenology of the plants in the stands that were studied.

In stands that were sampled at various times of the year and at different locations, the stages in development of the plants were different. For the stands sampled early in the season those plants maturing later were not sampled, and some of the earlier developing plants were not sampled in those stands that were sampled at a later time of the year. Genera that provided consistent difficulty were Aster, Carex, Solidago, Salix, and Poa. No reliable means of vegetative identification could be established. The unflowering or fruiting plants were identified by comparing the undeveloped ones to those that were flowering in the stand if this was possible. In some of the earliest stands, however, none were flowering and later trips to the stands afforded collection of unknown species. These were then compared to the earlier stages of development collected with the first visit, and identification was then made. In the case that the stand was not revisited the plant was left at the generic level.

In some cases with species in the Cyperaceae the plants did not flower in the shade, and if there were two of the same group, viz.

Vesicareae, that occurred in the stand and looked quite similar vegetatively, the non-flowering ones were left at the generic level.

There were seventeen species of the genus Carex that were collected in the sampling of the mature bottomland stands. In order to become familiar with this genus, the entire collection of the University of Montana Herbarium was surveyed during the winter and spring of 1964 before the field work began. The county, elevation, and the exact location of the collection in the herbarium were recorded. This summary is deposited with the Plant Ecology Laboratory. Many of the specimens in the herbarium collection were varified by F. J. Hermann, and those that were collected in the field were compared to this collection in the herbarium.

Populus trichocarpa is the only native poplar to occur in western Montana (White, 1951; Morris *et al.*, 1962). Hitchcock *et al.* (1964) state that around Flathead Lake *P. trichocarpa* hybridizes with *P. deltoides* var. *occidentalis*. In the communities sampled all of the trees were considered to be *P. trichocarpa*.

If unknown plants were obtained in the stands these were brought back to the laboratory and they were pressed for later identification. A collection of the plants made from the stands is deposited at the Plant Ecology Laboratory. The nomenclature follows that of Hitchcock *et al.* (1964) for the Salicaceae through the Compositae, and Davis (1952) for the Polypodiaceae through the Orchidaceae. The list of the plants found in the stands is given in Table 10.

DESCRIPTION OF METHODS

Field Methods: During the months of June, July and August of 1964 a phytosociological study was made in the lowland deciduous forests of western Montana.

Since the word "stand" will be used frequently in the discussion it is necessary to define this word first and then describe the methods used to choose the stands and secondly the method used to describe their characteristics. Greig-Smith (1964; p. 134) defines a stand as "any area the vegetation of which has been treated as a unit for purposes of description." This will be the manner in which this term will be used in this paper.

There were a number of criteria which had to be satisfied before a particular area was sampled. First, the area had to be composed of hardwood trees for an area of at least 3 acres. This small area was used because of the numerous instances along the bottomlands where hardwood stands may occur as a narrow strip to proximal coniferous vegetation. These fringe areas of hardwoods, however, often are quite well developed in the tree size class and although many of these small areas are local, they are characteristic of the bottomland hardwood type and are part of a description of the bottomlands despite their small extent.

The second criterion for selection of the stands was that they were required to be undisturbed by cutting, fire or grazing within approximately the past 10 years. This test for stand selection eliminated the greatest number of areas. This was especially true for those stands which were the oldest, and had been invaded extensively by ponderosa pine or supported older stands of black cottonwood or trembling aspen. It is for this reason that later successional stages of trees were not sampled. In those areas which have become dry enough and free from yearly inundation, cattle and horse use is usually present.

The third criterion for selection involved the aspect of overstory homogeneity. This, as Curtis (1959) states, is a difficult concept to understand, but it involves the uniformity of distribution, age and species in a stand which is to be sampled. Greig-Smith (1964) in discussing this concept cites Goodall (1954) who states that if a community has real existence, it should have compositional homogeneity inside the community. However, Goodall states that complete homogeneity does not exist, but that there may be a greater degree of homogeneity in one stand than two different stands. The homogeneity of the overstory trees was a primary characteristic of the stands. This was not the case for saplings and understory plants.

The intent was to sample as wide a variety of bottomland stands as possible. The criterion for determining different types was based on species composition, physiognomic site, age according to the tree size, and tree density, dominance and frequency. This obviously introduced subjectivity and personal bias into the stand selection. One point should be made clear here. The fact that a certain type of stand, such as a _P. tremuloides_ stand, was the only bottomland stand from a particular region, does not infer that this was the only type of stand that occurred in that region. For example, _P. tremuloides_ stands occur on the edge of oxbow lakes in the region of Missoula and the Bitterroot Valley, but there were no representatives of this type of stand sampled because of the heavy land use and the inability to find ungrazed stands of this type in the Missoula region. Undisturbed stands of this type were found in the Blackfoot and Flathead Valleys, so they were sampled. Likewise, floodplain stands occur in the Blackfoot and Middle Fork of the Flathead River, but these were not sampled.

One of the most important factors to recognize when planning a sampling study is the distribution of the plants to be sampled. Odum (1956) recognizes three broad patterns for the distribution of the individuals within a stand: "random, uniform (more regular than random), and clumped (irregular, non random)" (p. 213). Random distributions in plants and animals are rare in nature. Uniform distribution is more common in animal populations than in plants where territoriality may separate individuals evenly (Nice, 1941). The aggregated or clumped situation is the most common (Odum, 1956). Curtis and Cottam (1956) state that if trees are noticeably clumped and have spaces that are noticeable between them, neither the quarter nor the quadrat method will give accurate density values.

Oosting (1956) states that sampling conserves both time and labor and if an adequate sample can be obtained it can be extremely useful in a vegetational study. It has been mentioned above that most natural vegetation is clumped. Aggregated populations are notably difficult to sample. Kershaw (1959) and Greig-Smith (1952 and 1964) and others have felt that there is a decline in the contagion of a stand as the stand becomes more stable and the pioneers decline in abundance. Though there is a variation from one stand to another, the degree of non-randomness is related to the age of the stand

(Whitford, 1949). Whitford also infers that the amount of contagion declines with the increasing age of the stand. There are a number of aspects of this present discussion which seem to be applicable to the bottomland vegetation. These can best be illustrated later when analyzing the plants and their distribution in the bottomland communities.

The trees and saplings were sampled by the quarter method (Curtis and Cottam, 1956). This is a distance sampling method and the closest trees to a randomly selected point are recorded. This method is faster than the quadrat method, requires less workers, and the sample size does not have to be adjusted for vegetation type (Curtis and Cottam, 1956). The method is based on the theory that the distance from the point to the four trees when averaged will give the square root of the mean area occupied per species individual. The size of the area that each individual occupies is M^2. The twenty points that were sampled by the quarter method were distributed every 20 paces along a predetermined line. At each point the species, distance from the point, and diameter at breast height were recorded for the closest trees and saplings in the four quadrants. A six inch direct vision range finder was used to determine the distances from the points to the trees in the four quadrants. These data were then recorded in a tape recorder and later transcribed onto field sheets.

The feature that was used to differentiate between trees and shrubs was a subjective one. In this study all species which commonly reach a size of four inches DBH or larger were considered as trees. It is now believed that a better criterion might have been to consider as trees only those species that ordinarily obtain a major dominant role in the stands. This would eliminate species such as *Alnus incana*, *Betula occidentalis*, *Crataegus douglasii*, *Acer glabrum* and *Prunus virginiana* from the tree category. These species were never observed to reach a major dominant role in communities other than early secondary successional ones, although individuals of these species frequently achieve diameters greater than 4 inches DBH.

One problem became apparent upon analysis of the stands when *Alnus*, *Betula*, *Crataegus*, *Prunus* and *Acer* were treated as trees. Due to their greater densities, *Alnus*, *Betula*, *Prunus*, *Crataegus*, and *Acer* often were contacted in the quarter method more frequently than the saplings of the major dominant species such as *Populus trichocarpa*, *Pinus ponderosa*, *Picea engelmanni* or *Populus tremuloides*. Therefore, a true picture of the reproduction of the dominant trees is obscured.

An accurate method for measuring the density frequency and dominance of these arborescent shrubs needs to be devised. Although a third set of measurements taken for these arborescent shrubs such as *Prunus* and *Crataegus* might be accurate, the data obtained by the quarter method for such genera as *Alnus*, *Betula* and *Acer* would not be a valid representation of the tree density for these species because of their many stemmed spreading physiognomy. Dominance is not usually determined for saplings because this category is based on DBH, and saplings do not vary greatly in diameters. However, an investigation for a sampling method on alder, birch and rocky mountain maple should include a method for estimating dominance of these species. This might involve a method for determining the dominance of the whole multi-stemmed clump. The size of the clumps is believed to influence greatly the understory herbs of the stand.

If the bottomland study is to be continued, it is believed that reclassifying Alnus, Acer, Crataegus, Betula and Prunus into an arborescent shrub category and sampling these tall shrubs, saplings and trees as three different classes would be beneficial. However, since the sampling method classified these species as trees and saplings they will be considered in this category for discussion in this thesis.

It has already been stated that the overstory in these stands was homogeneous. However, this does not apply to the saplings, especially in the case of Alnus incana, Betula occidentalis and Salix alba. These arborescent shrubs were often extremely contagious in their distribution, being restricted to low, wet areas. Therefore, high densities of these species should be considered to be indicative only of moister conditions. The precision of the sample when dealing with these species is believed to be low because of the difficulty involved when sampling aggregated populations. This is true except in some cases where a fairly homogeneous distribution was present. This latter circumstance occurred in some of the tributary stands.

The herbaceous plants and the shrubs were sampled by the use of a one meter square quadrat. Frequency was determined for all shrubs and herbaceous plants in the stands. The frequency is the percentage of quadrats occupied by a given species per total number of quadrats in the sample. The meter square quadrats were sampled at each of twenty points. The one meter square quadrat has been used by Habeck

(1963) in other studies of forest communities in western Montana, and comparison of species composition in the stands that he sampled and those of the present study will be made in the future.

Oosting (1956) states that frequency values from a stand sampled with one sized quadrat cannot be compared with those obtained from a stand with different sized quadrats. Numerous workers have shown that in different habitats different sized quadrats give more accurate results. The frequency is a product of the size of the quadrat and the dispersion of the plants. Oosting notes that the use of frequency as a single value without density of the species has been unsatisfactory when attempting to understand the basic community structure. Curtis (1959; p. 76) states that "rare species are encountered an insufficient number of times to give statistical reliability, and the sum of the resultant errors tends to reduce the overall reliability of the entire complement."

One final and important point should be made here. Curtis and Cottam (1956) state that if trees are noticeably clumped neither the quarter nor the quadrat method will give accurate results. Kershaw (1959), Greig-Smith (1952 and 1964) and others have felt that there is a decline in the contagion of a stand as the stand becomes more stable and the pioneers decline in abundance. Since many of the main river stands were located on active floodplains and the edaphic conditions are continually subject to disturbance, these stands are not stable and in many cases the vegetation is extremely aggregated. It is for this reason that the frequency values for species in the disturbed stands should be used with less emphasis in analyzing the stands than the tree characters. The trees are also subjected to extreme environmental changes, but they are less susceptible to contagion because of their greater ability to withstand stream action.

A presence list was taken in each stand. This included the recording of all vascular species that were present in the stand before starting to sample.

Soil samples were collected at each stand. The A layer and the B layer were collected at three different points along the sampling line, usually the second, tenth and eighteenth points. These were then placed in plastic bags and brought to the plant ecology laboratory where they were air dried. The soils were then sieved through a 2 mm screen. The samples were sent to the University of Wisconsin Soils Testing Laboratory where the soils were tested under the direction of Prof. H. H. Hull. The soils were extracted with 0.3N HCl. P, K, Ca, NO_3 and NH_3 were determined. Soil pH was determined with glass electrodes and the organic matter was determined by chromic acid digestion. A subsample was retained at the plant ecology laboratory at the University of Montana, this was used to measure the water holding capacity in the soils laboratory at the U.of M. School of Forestry. The method followed that of Anon (1961).

Laboratory Treatment of Data: The field data sheets were transcribed onto a laboratory analysis form adapted for the analysis of forest communities in northwestern Montana. The tree diameters were converted to basal area by the use of the conversion table given in Curtis and Cottam (1962). These values, as well as the distance data that were obtained from the quarter method, were then converted for the tree data into relative frequency, relative density, relative dominance, importance values (summation of relative frequency, relative density and relative dominance) and total tree density per acre. The sapling data were converted into relative frequency, relative density, importance value (summation of relative frequency and relative density) and total sapling density per acre. This was done for each of the tree and sapling species contacted in the quarter method. Curtis and Cottam (1962) explain the derivation of these quantitative features.

The percentage frequency for the understory plants was also tabulated from the field frequency sheets. Files were then developed for each stand which contained the tree, sapling, and herb summarized data, and the computations used to derive these final quantitative characters of the community. These files also contain the soil data which were summarized on a form.

Table 11 was constructed to arrange the stands into classes based on their tree size distribution. This table was then divided into four quartiles. The stands with the largest trees were in the fourth quartile and those with increasing smaller tree sizes were in quartiles 3, 2, and 1. Quartile 1 included the stands with the smallest trees. These quartiles in Table 11 will be referred to later in the paper. Presumably, stands with larger trees are older, but this is complicated to some extent by the life span in different tree species.

RESULTS

Introduction: An attempt is made to classify the bottomland stands that were sampled. The stands are arranged in order according to the similarity of the dominants found in the stands. If the stands are classified by their first dominants, five classification types would result. If the first and the second are used eleven types would result. The third and the fourth dominants would yield nineteen and twenty types respectively. Therefore, it is evident that with this type of classification system there would result almost as many types as there are stands in the phytosociological analysis (see Tables 7 and 9).

Composition of Stands Dominated by *Populus trichocarpa*: *Populus trichocarpa* occurred in communities sampled either as a pure stand or in association with nine tree species, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Populus tremuloides*, *Picea engelmanni*, *Thuja plicata*, *Alnus incana*, *Acer glabrum*, *Crataegus douglasii* and *Betula occidentalis*.

Populus trichocarpa was the dominant tree in 16 out of the 23 stands that were sampled (see Tables 7 and 9). In two stands black cottonwood is the only tree present. These were in the open floodplains. In four other stands there is only one other tree species occurring with black cottonwood. In two stands there are three tree species growing and in the remaining eight stands where *P. trichocarpa* is the dominant, there are four or more tree species recorded. Ponderosa pine occurs with black cottonwood more often than any other tree.

Saplings of black cottonwood obtain their highest importance value in stands 21 and 22 (see Tables 8 and 9). These were located in the open floodplains. The highest density of saplings for this species is in stand 7. This is a younger stand composed of smaller tree sizes (see Table 11). The density of saplings for this species generally declines as the stand ages and grass competition and lack of mineral soil prevent seedling establishment by sexual means. In older stands reproduction by this species is primarily by root sprouts.

In the stands that are dominated by black cottonwood, the two most predominant shrubs show less variation than the herbs. *Rosa woodsii* and *Symphoricarpus albus* are the most common shrubs obtaining highest frequencies. At least one of these shrubs is among the first two dominant in all of the cottonwood stands. Others can be seen in Tables 8 and 9. The understory herbs are more variable but the most common are *Agropyron repens*, *Poa pratensis*, *Poa compressa*, *Osmorhiza chilensis* and *Galium triflorum*. The grasses are more dominant in the major floodplains and in the canopy openings of the tributaries and the other species are more dominant in the shadier, moister and more protected tributaries.

Composition of the Stands Dominated by Picea engelmanni: There are two stands that were dominated by *Picea engelmanni*. The other trees occurring in the spruce stands are: black cottonwood, choke cherry, lodgepole pine and Douglas fir.

The only two saplings that are common to both of these stands are cottonwood and spruce. The saplings with the highest importance value in one of the stands is *Juniperus communis*, and in the other is *Prunus virginiana*. The other sapling compositions can be seen in Tables 8 and 9.

The shrubs and the herbs each show different combinations of dominants for the species with the highest frequency. One stand consists of a snowberry - rose association and the other consists of a rose-buffaloberry association. Only one of the two most common herbs, Equisetum fluviatile, is common to both of the spruce stands.

Composition of the Stands Dominated by Populus tremuloides: There are three stands that are dominated by trembling aspen. In the first two stands, cottonwood is the second dominant. However, in the third stand, 16, cottonwood was not obtained in the sample by the quarter method because of its low density. It was only recorded as present in the stand, for scattered individuals do occur in the moister sites of this stand. The third and fourth dominants in these stands dominated by trembling aspen are not similar (see Tables 8 and 9).

For those herbaceous plants that obtain highest frequencies in the aspen stands, there are none common to all of the aspen stands. Those that obtain first dominance in the aspen stands are Carex retrorsa, Smilacina stellata and Berberis repens. It is felt that some sampling error is introduced here, for stand 19 was covered by a layer of silt that reached 4-5 inches in depth in some places. Therefore, this obscured the understory from vision within the sampling quadrat. Otherwise, the understory in these stands, especially between stands 19 and 18, under normal conditions, might be more similar. The silting was a product of the severe floods of 1964 in the Kalispell region.

Composition of the Stands Dominated by Pseudotsuga menziesii: There is one stand dominated by Douglas fir. The composition of this stand can be interpreted from Tables 8 and 9.

The most striking difference in this stand's composition lies in the occurrence of Abies grandis. Grand fir occurs in only one other stand that was sampled, stand 23 in the region of St. Regis. Cottonwood and river birch are the only other species that stand 6 and stand 23 have in common. These two species, cottonwood and river birch, are among the most ubiquitous for the bottomlands in western Montana. Therefore, the indicator value, provided by these two species for the occurrence of grand fir, is extremely low. The indicator value provided by Pseudotsuga menziesii for the occurrence of grand fir is also very low, for Douglas fir occurs in many stands where Abies grandis is not present. Some of these occurrences are shown in Tables 7, 8 and 9.

Composition of Stands Dominated by Thuja plicata: One stand, 44, was dominated by this species and one other stand, 23, contains cedar as a third dominant. The composition of stand 44 is given in Table 8. One tree, Tsuga heterophylla, occurs in this stand and does not occur in any other stand. The remaining composition of this stand, dominated by Thuja plicata, can be interpreted from Tables 8 and 9.

The two stands that contain cedar have few other compositional characters in common. The few characters that they do have in common are: they each contain cottonwood trees, each contains snowberry and the herb with the highest frequency in both of these stands is Smilacina stellata. The most interesting character is that Smilacina stellata has a high constancy for all of the stands sampled, but it is the herb with the highest frequency in these two stands.

Composition of Stands Containing Pinus ponderosa: Tables 7 and 8 show that there are ten stands that contain ponderosa pine. In three of these stands, ponderosa and black cottonwood are the only trees present. For the ten different stands that contain ponderosa pine there are eight different associations that occur when the tree data alone are analyzed and used for designating the associations. The increasing number of types that develop with additional dominants used in the classification are shown in Table 7. If the sapling data are used, ten different associations can be described (see Table 8). The number of associations, therefore, is the same as the number of stands that contain *Pinus ponderosa*.

Classifying the bottomland stands is made more difficult by the fact that cottonwood has a wide geographic range of tolerance. It therefore may develop into, or be present in, many different types of communities, depending upon the surrounding vegetation which is governed in turn by local geography, climate, and topography. Further variation is introduced in the wider floodplains which are an "open" community (Raup, 1964). These communities are in a constant state of environmental change; therefore, the vegetation, similarly, becomes organized into many different combinations of species due to the disturbance factors imposed by the rivers.

Variability and Classification of Bottomland Stands: The most striking aspect in the analysis of the bottomland stands is the variability demonstrated by the tree composition. The brief discussion above demonstrates this point. For the twenty-three stands that were sampled, if only the first dominants are used to classify the bottomland stands, five communities or types could be designated. If the second dominant is used, eleven types would result. There is an increasing number of types as more of the dominants are used for the classification system. If the third dominant is used, nineteen types result, and if the fourth dominant is used, twenty types result. Table 8 demonstrates that if the saplings are used to classify the communities, twenty-two types result, and if the shrubs are used, twenty-three types result for the twenty-three stands. By including the herbaceous plants in the description even more compositional variation is apparent (see Table 8).

The purpose in demonstrating this compositional variation is to show that a description or classification of these bottomland stands by the use of an approach such as that employed by Daubenmire (1960, 1946 and 1943) would be difficult and artificial because there would be as many different community types or associations as there are stands analyzed.

Kirkwood (1922) feels that the distribution of the forests in western Montana is a result of geography, topography and climate. Bottomland vegetation in western Montana is also believed to be greatly influenced by degree of disturbance imposed by the amount of flooding of the stands. Therefore, if the vegetational composition of these bottomland stands is compared, the vegetation could be expected to form a continuum corresponding to environmental gradients constructed of elements of the environmental factors mentioned above viz., geography, topography, climate, and degree of inundation. The stands that are the most alike vegetatively would be expected to be the result of similar history environmental conditions, and consequently would be found proximal to each other on an environmental gradient. Conversely, when the vegetation is significantly dissimilar, the environmental conditions would be expected to be dissimilar, and the stands would be found further apart on an environmental gradient. Similar successional stages of a vegetational community found at one position on the environmental gradient would not be expected to be the same as that found at another position on this same gradient. Stands found at different positions on this environmental gradient would not necessarily be expected to eventually possess the same vegetational composition. Stands sampled at different positions on an environmental gradient, therefore, would show marked variation in their phytosociological characters, even if they were, theoretically, in the terminal stages of succession.

Ordination Construction: "Classification involves arranging stands into classes, the members of each of which have in common a number of characteristics setting them apart from the members of other classes ... Ordination is a more recent development.... It stems from the concept of vegetation as a continuum (Greig-Smith, 1964; p. 158). Ordination attempts to show, by ordering the stands along various axes, the spatial relationships between the stands. The stands which are most similar will be closest together in the ordination. Their similarity will be a result of likenesses in phytosociological characters which are the result of similar environmental conditions. The phytosociological characters are obtained from the analysis of the data taken by the various sampling methods.

There have been, in the past few years, a number of workers that have used this ordination technique to describe and analyze plant communities (Ayyad and Dix, 1964; Bray and Curtis, 1957; Loucks, 1962;

Beals, 1960; Curtis, 1959; Goodall, 1954). This method, which arranges a series of stands along compositional gradients, may demonstrate a vegetative continuum (Curtis, 1959). These gradients of vegetation often can be correlated with environmental gradient factors (Curtis, 1959; Loucks, 1962; Ayyad and Dix, 1964; Choate, 1963). This method of vegetational analysis is different from the techniques used by Daubenmire (1952) in his classification of the N. Rocky Mountain vegetation into distinct climax associations. "Classification implies discontinuity in composition not only between concrete units in the field but also between abstract classes into which all vegetation may, theoretically, be placed. Ordination implies continuous variation in composition, though not precluding discontinuity in the field corresponding to discontinuity in determining factors" (Greig-Smith, 1964; p. 158).

The communities were compared by using an Index of Similarity, $C = \frac{2w}{a+b}$ (Bray and Curtis, 1957) where _a_ is the sum of the quantitative values in one stand, and _b_ is the sum of the quantitative values in a second stand, and _w_ is the sum of the quantitative values that are common to both stands. The Index of Similarity was determined by the use of a computer program supplied by Dr. Robert Ream from the University of Wisconsin and modified by Professor John Peterson from the University of Montana computer center.

The formula, $\frac{2w}{a+b}$, was used to establish the Index of Similarity values between twenty-two stands containing _Populus trichocarpa_. One exception, stand No. 16, was not included in the ordination because, although it had _Populus trichocarpa_ present, no trees were tabulated with the quarter method because of their extremely low density. Because the ordination involved communities principally dominated by *P. trichocarpa*, the inclusion of a single stand (No. 16) in the ordination that had only a minor component of *P. trichocarpa* tended to clump the *P. trichocarpa* stands. However, this stand offers some interesting comparisons with a vegetative study done by Lynch (1955) in Glacier County and also the understory data provide interesting comparisons to other stands in the present study.

It has already been stated that the Index of Similarity was used to compute stand similarities. All of the tree, sapling, understory and soil data that were gathered were not used in the comparison of the sampled stands because of the limited storage capacity of the computer and because of the subjective feeling that certain data were more prone to sampling error and were less precise. The sampling error and the low precision of some data, *i.e.* soils and understory, are mainly a result of the disturbed and heterogeneous character in many of the communities studied, and the type of sampling method used. The data that were used were therefore subjected to personal bias. The characters used appear in Table 14. Because of the belief that the understory plants were less representative of the characteristics in the stands due to the problems already discussed in sampling and disturbance, there were only 10 characters used from the understory data and 85 from the tree data. There were therefore a total of 95 characters used to compare the stands. A total of 2,090 comparisons were necessary to compute the spatial arrangement of the twenty-two communities. In a separate undertaking the understory plants were also compared, using 61 species (see Table 13).

The arranging of the stands and the construction of a two dimensional ordination was done with the method described by Beals (1960). The absolute values of various community characteristics in each stand were converted to quartile values (Bray and Curtis, 1957). This permitted the study of the behavior of each species in relationship to the stands in the ordination. In order to compute the quartiles, the highest quantitative value for a particular characteristic is divided into four equal quantities; the lowest 1-25%, the second 26-50%, the third 51-75%, and the fourth 76-100%. These were then distinguished as quartiles I, II, III and IV. To illustrate these relative ratings in the ordination diagrams, four different sizes of circles were used to represent the different quartiles. The smallest circle was used for quartile I and the largest for quartile IV (see Fig. 2). In a few cases where the highest value was much higher than the other values, and thereby tended to group all other values into only the first quartile, the highest value was given an automatic quartile IV rating, and then the second highest value was used to compute the quartiles of the remaining values. When this technique of quartile determination has been used in the data presented in this paper, it is so indicated.

ORDINATION RESULTS

General Interpretation of Physiographic Areas in the Ordination: The ordination constructed from the tree data is given in Figure 3. It has already been stated that classification into discrete, vegetative groups cannot be made because of the variability in community composition. However, it appears that certain communities of the bottomland hardwoods are more closely related floristically than others, when many different phytosociological characters are compared. These relationships appear to be controlled by certain environmental gradients. Therefore, certain physiographic groups are arbitrarily established in order to discuss the distribution of the communities in the ordination. It is emphasized that this is an artificial categorization of the stands, and that in spite of the relative similarity in the phytosociological characters among these artificial groups, there still exists the significant variation as previously described.

There are smaller phytosociological differences between stands found in similar physiographic areas of the ordination. The smaller differences between individuals in the same physiographic units are perhaps caused by small differences in the environment within each of the physiographic groups. Significant dissimilarities among the phytosociological characters, between different physiographic units, are probably due to greater differences in the environments between several physiographic units.

The first physiographic category that is delineated in this ordination includes the group of stands which obtain the highest values on the X- axis, and the lowest values on the Y- axis. These are stands 23, 1, 2, 5, 6, 3, 18, 44 and 4 (see Fig. 3). These are the tributary and oxbow communities located mostly in narrower valleys, with the exception of stand 18 (see Table 6). These stands are located in the less severely disturbed, and less frequently inundated sites. They are found at elevations from 2500-4000 feet. Generally, these stands have soils with a greater soil water holding capacity and deeper organic layers. (see Fig. 4).

The second physiographic group includes stands 8, 10, 24, 9, 7, 22, and 21 (see Fig. 3). These stands are located at elevations ranging from 3000-4000 feet in the more open valleys and usually in the floodplains of the wider rivers (see Table 6). They are subject to the greatest flooding and inundation of any of the stands, and generally have lower water holding capacities and lower organic matter in the soils (see Fig. 4).

The third group contains stands 14, 13, 12, and 15 (see Fig. 4). These are generally the highest elevational stands that were sampled viz. 4000-5000 feet. The stands in this third group are located on major river systems, but the valleys containing these stands are moister and cooler than those that contain the second group of stands (see Table 6). These stands are probably subjected to only inundation from flooding in extremely high years. The soils have a low soil water holding capacity and low soil organic matter content (see Fig. 4).

Stands 4, 19, and 20 do not appear to fall specifically into any one of these designated physiographic groups (see Fig. 3). They are either very small floodplains or very large tributaries. Stand 4 is located on Lolo Creek and is apparently rarely disturbed by inundation. It does have certain features of the environment that make it more floodplain-like than some of the other tributary stands that occur in smaller valleys. An oxbow remnant in the middle of this stand indicates that the creek at some time in the past probably divided this stand. This meandering behavior of the river is more similar to that of the wider rivers and in this stand left a minor floodplain. Also, the clearing of land for farming in the vicinity, and the wider valley, may have made the conditions more xeric and similar to conditions present in the floodplains. This might explain its close approximation to the floodplains in the ordination. The high importance values for P. trichocarpa, both trees and saplings, the higher percentage of some of the grasses, and the lower frequencies of some of the herbs more common to the more protected tributary stands may be attributable to the more open and floodplain-like nature of this stand. This stand also has less litter covering the forest floor than some of the tributary stands, but the lack of frequent inundation resulting in a high water holding capacity of the soil and the medium organic matter of the soil may be indications of some of the basic environmental factors causing some tributary floristic affinities.

Stand 19, in the ordination, is more closely aligned with the floodplain stands. This stand is located in the upper Flathead Valley at the edge of an oxbow lake. It is more difficult to interpret, for it was covered by a layer of clay flood-sediments that buried the herb layer. The closer floristic affinity to the floodplain stands may be due to the similarity of environmental conditions that exist in open valleys whether the stands occur on an oxbow or a floodplain (see Fig. 3). This stand does not occur on a disturbed site such as a floodplain, and it contains a higher percentage of P. tremuloides than most active floodplains do in western Montana (see Table 8). Many environmental conditions such as light and wind action, because of its situation in an open valley, may be quite similar to the floodplains (see Table 6). This would cause stand 19 to develop a comparable composition to the floodplains. The composition of this stand and those found on the active floodplains is not completely similar. If it were, stand 19 would be found among the floodplain stands in the ordination. Probably, many of the environmental conditions are different between stand 19 and most of the active floodplain stands, and these are perhaps the cause of the difference in the floristic composition. But the conditions are probably more similar between stand 19 and the floodplains than they are between this stand and those found in the narrower tributary valleys.

Stand 20 is located on the Middle Fork of the Flathead River. It is probably not subjected to flooding except in above normal run off years. Floristically it is more closely related to the tributary stands than the floodplains. The occurrence of high percentages of Prunus virginiana, and Crataegus douglasii, which do not obtain high importance values in the active floodplains, may be a major factor causing this spatial distribution of this stand (see Table 6). Another affinity apparently exists between this stand and the higher elevational stands, especially stand 14. Picea engelmanni reaches its highest importance value in stand 20. Therefore, it is floristically related to stand 14 which contains the second highest importance value for Picea engelmanni.

Some environmental factors for stands 20 and 14 _viz._ summer temperature and moisture appear to be similar. The occurrence of spruce in the bottomland stands is fairly restricted, and indicates specific requirements for its presence. This species does not occur as widely as species such as _Pinus ponderosa_ or _Pseudotsuga menziesii_.

Ordinational Gradients: The discussion of the different characteristics of the physiographic units of the ordination makes it possible to suggest some environmental gradients that may be correlated with the distribution of the stands in the ordination (see Fig. 3). The strongest gradient appears on the Y axis or the vertical axis. The vegetational gradient demonstrates that the tributary stands have the lowest values on the Y axis. These are the stands that have lower importance values for _P. trichocarpa_. From what has been said earlier about the autecology of black cottonwood, this species appears to be maintained in a disclimax because of the disturbance factor imposed on the community by the river. Therefore, the most obvious environmental gradient shown in the ordination is a disturbance gradient. Those stands with lower values on the Y axis are less disturbed and found on smaller tributaries that are not subject to the extreme water erosion under normal conditions.

The stands that have high values on the Y axis are the most highly disturbed and therefore cottonwood can achieve and maintain high importance values here. As the stands become more stable, the conditions become more favorable for the establishment of conifers. As this happens the stands would be expected to attain phytosociological characters that might give the stands lower values on the Y axis. It is believed, however, that the successional movement on the Y axis could not approach completely the phytosociological character that is found in the narrower ravines and narrow tributary valleys. This is because of the more exposed physical position of the cottonwood stands that are found in the open valleys. The open valley stands are subject to greater drying action from the wind and the higher heat in these open valleys also decreases the moisture in this site both in the atmosphere and in the soil. Lack of arborescent shrubs in the open floodplain would also discourage comparable phytosociological characters to develop, particularly in the understory herb layer.

The floodplain stands found in pockets along a mountain would be expected to be found in the ordination closer to the tributary stands because of the closer environmental similarity to the tributaries. The further into the open valley a floodplain stand is located and the more disturbed the site, the lower will be its similarity to the moister ravines. The same gradient is seen in the tributary stands and the more open, dry and disturbed the tributary, the closer the composition will be to a floodplain stand viz. stand 4.

Although some workers (Bray and Curtis, 1957) have noted a possible correlation between soil nutrients and community composition, this is not the case with this study. The data appear in Table 17. The most apparent characteristic of these soil data is that the nutrients are the least variable within the tributary stands, and within the stands found on the South Fork of the Flathead River. The reason for this may be that the tributary stands are the least disturbed, permitting homogeneous soil development. The South Fork stand soil similarity is probably caused by the relatively uniform nutrient load in the flood waters regardless of the stand position on the river. The heterogeneous nutrient composition of stands on the Bitterroot, Clark's Fork and Flathead Rivers is probably a result of greater civilization and land use along these rivers. Local deposits from fertilized fields and sewage may cause local differences in nutrient load of the rivers in these inhabited areas.

The strongest environmental gradients influencing the vegetational composition in the stands include disturbance and topography. The disturbance is necessary for maintaining pure stands of cottonwood, and the topography influences such environmental factors as moisture and temperature. The narrower valleys and the tributary stands in western Montana are more closely related and the open floodplain stands are at the other end of the environmental and vegetational gradient.

Composition of the Tributary Stands: The tributary stands 6, 23, 1, 3, 5, 2, 18, and 44 have higher importance values for *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, *Abies grandis*, *Betula occidentalis*, *Alnus incana*, and *Acer glabrum* (see Figs. 2 and 5). These stands have relatively low importance values for *P. trichocarpa* (see Fig. 2), but generally this species obtains its greatest size in this group of stands (see Table 13).

In the region where various sized water courses flow near the montane forests, black cottonwood often occurs in communities with coniferous members of these forests. In stand 6, *Populus trichocarpa* is restricted to a narrow strip adjacent to Bass Creek. The vegetation soon becomes completely coniferous at greater distances from the stream.

This is the closest community to a ravine that was sampled. Any narrower distribution of cottonwoods than exemplified by this Bass Creek stand makes it difficult to obtain a sample from a "homogeneous stand" of trees. However, these types of stands do occur. There are scattered trees of cottonwood which occur in the headwaters of many mountain ravines, but these were not sampled in the study because of the low density of trees and because the nature of the quarter sampling method makes it difficult to sample a narrow strip.

Although in the bottomland hardwood forests Pseudotsuga menziesii seldom represents a very predominant species, in the tributary and ravine stands, like No. 6, these usually support the highest importance value for this species. However, scattered individuals may occur on islands and in the open valleys of the larger rivers.

Thuja plicata and Tsuga heterophylla were restricted geographically to those cottonwood tributary stands found in areas of higher precipitation (see Table 6). Thuja plicata occurred in one stand in Mineral County, but it did not occur in association with Tsuga heterophylla in this stand as it did in the Glacier County stand. The ordination demonstrates the more restricted occurrence of Tsuga heterophylla (see Fig. 5).

Abies grandis had somewhat the same behavior as Thuja plicata, for it was found in the narrow, wet, cool ravine sites (see Fig. 2). It was not as restricted to areas of high precipitation as was red cedar and hemlock. Grand fir occurred in the narrow tributary ravine of stand 6 in the Bitterroot Valley where cedar and hemlock were not found growing with cottonwood.

Alnus, Acer, and Betula, although they reached their highest importance in the tree category in this group of stands, were more often encountered in the sapling category.

The tree densities of these stands varied from 193.5 to 53.2 trees/acre (see Fig. 6). P. trichocarpa reaches one of its lowest densities here with 23 trees per acre. The density of this species in this group of stands is much lower than in those areas on the major rivers (see Fig. 6). Pinus ponderosa and Acer glabrum reach their highest densities in this group of stands (see Fig. 6). Alnus incana and Betula occidentalis have similar behavior patterns to these species in the ordination. A fact mentioned earlier, however, should be recalled: old aged ponderosa pine stands, situated in the wider valleys, were not sampled because of extreme grazing disturbance.

Sapling density in this tributary type is generally higher than in the floodplain stands of comparable age (see Fig. 7). Acer glabrum, Prunus virginiana, Alnus incana, Betula occidentalis, Crataegus douglasii, and Populus tremuloides are the most common and reach their highest densities here (see Figs. 7 and 8). Prunus, Alnus, and Betula are more ubiquitous than the other two. Acer glabrum was the most restricted within the compositional ordination in this group of species (see Fig. 7). Tsuga heterophylla and Thuja plicata are restricted to geographic areas of higher precipitation.

Prunus virginiana is, with the exception of river birch and cottonwood, the most ubiquitous sapling in all of the bottomlands studied (see Fig. 8). It reaches its highest density in the tributary stand 5. It does occur, however, with high densities in those more mature floodplain forests that are not subject to extreme, and consistent flooding, such as stand 20. It often occurs in the mature floodplain forests dominated by ponderosa pine in the Bitterroot and the Missoula Valleys. Its behavior in the ordination indicates its affinity for less disturbed sites in the open valleys and the narrower tributaries. Alnus incana is usually restricted to low areas or to aggregated groups along streams which occur throughout the bottomlands. In the tributary community where it obtains one of its highest importance values (stand 3) an irrigation ditch runs across the hill above the stand and provides an extremely wet site. This species does not appear to be restricted to either the oldest or youngest stands, but occurs in the wettest areas in both types. It often reaches high densities in wet, early successional back water areas of the tributary streams. Stand 3 is the closest example to this type of site, although from the size of the trees given in Table 11, the density of alder would not be expected to be as great as this. The influences exerted on the community by the irrigation ditch apparently has caused a reduction in some of the species such as Acer glabrum, and favored species such as Alnus incana and Cornus stolonifera, which occur in moister sites.

In the ordination alder reaches its highest densities in the position of the gradients where moisture is greatest for the longest period of time (see Fig. 7). In the open valleys, and drier sites of the floodplains, the density of this species declines.

Betula occidentalis, Prunus virginiana and Alnus incana obtained their highest sapling densities in stand 5. Table 11 indicates that this is the youngest tributary stand studied. The density of alder and birch appears to be more dependent on the presence of moisture in the stand, and not on the age of the stand. *Prunus* declines in importance in the older tributary stands, but on the floodplains it increases in importance in the more mature and less disturbed forests.

Although *Crataegus* reaches its highest densities in the tributary stands, it also obtains high densities in the more mature stands that occur in the open valleys. These high densities in the more mature forests in the open floodplains are usually attained as thickets along lower areas. None of these communities were sampled in the study, but its relationship to the gradients shown in this ordination appears to be dependent on the disturbance factor. It occurs in some of the tributaries and the open floodplain stands that are least inundated and disturbed. In the most disturbed areas this species does not occur. The behavior of this species, however, is not as obvious as such species as alder, birch and cottonwood saplings. In some of the undisturbed tributary sites, such as stand 1, this species attains very low densities. This stand has a high importance value for ponderosa pine, but in another stand that does not have a high importance for ponderosa which is in the same drainage, and on the same creek, *Crataegus* attains its highest density. The behavior of this species is therefore difficult to interpret.

Acer glabrum was found in all of the tributary stands, except stand 3, which was the stand that had high importance of alder and birch and some of the shrubs associated with moister areas such as *Cornus stolonifera*. The absence of mountain maple in this stand could have been due to the extremely wet conditions imposed on this community by the irrigation water seeping from above the stand into the community.

Acer glabrum reaches its highest importance value in stand 1, which is being invaded throughout by *Pinus ponderosa*, and has the highest importance value and density for ponderosa pine, as well as the most homogeneous distribution for this species for any of the stands that were sampled.

The seedlings of *Acer glabrum*, *Betula occidentalis*, *Alnus incana*, and *Abies grandis* all reach their highest occurrence in this type of stand. *P. trichocarpa* seedlings are not common except as vegetative root sprouts. This may have been due to a number of factors. Lack of mineral soil and light may have been among the more important of these.

Twenty-five of the most common herb species for the tributary stands are given in Table 16. Some of these are also plotted with quartile values in Figures 9 and 10. Although there is considerable variation in herb frequencies, *Osmorhiza chilensis*, *Heracleum lantanum*, *Mentha arvensis*, *Urtica dioica*, *Thalictrum venulosum*, *Disporum trachycarpum*, *Actea rubra*, *Circaea alpine*, *Galium triflorum*, *Pyrola asarifolia*, *Polypodium hesperium*, *Aytherium felix-foemina*, *Angelica arguta*, *Berberis repens*, and *Equisetum lavaegatum* seem to be the most important herbs in this community type.

There are a number of herbs which show a high fidelity for stands 6 and 44. The herbs found only in stand 6 include *Hieracium albiflorum*, *Festuca occidentalis*, *Pterosposa andromedea*, *Coralorhiza maculata*, *Pyrola secunda*, *Boykenia major* and *Arnica latifolia*. Species occurring only in stand 44 are *Osmorhiza occidentalis*, *Aralia nudicaulis*, *Viola orbiculata*, *Rosa gymnocarpa*, *Galium aparine*, *Tiarella unfoliata*, *Dryopteris cristata*, *Botrychium virginianum*, *Goodyera oblongifolia and Melica subulata. There is one species that is common only to stands 6, 23, and 44. This is Chimphila umbellata. These three stands were each composed of a high percentage of conifers and were surrounded by coniferous forest. First dominant in stand 44 is Thuja plicata; in stand 6, Pseudotsuga menziesii, and in stand 23, P. trichocarpa. Third and fourth dominants in stand 23 are Thuja plicata and Abies grandis. Clintonia uniflora is common only to stands 6 and 44, and Trillium ovatum is present only in stands 3, 6, and 23. Stand 3 has two conifers as third and fourth tree dominants, Pseudotsuga menziesii and Pinus ponderosa.

Among the shrubs sampled in the study, Philadelphus lewisii, Sorbus scopulina, Rubus pariflora, Rubus idaeus, Holodiscus discolor, Amelanchier alnifolia, Rhamnus alnifolia, Ribes americanum, Ribes hudsonianum var. petiolare, Ribes setosum and Ribes lacustre, Menziesia ferruginea and Rosa gymnocarpa reach their highest frequency values in tributary stands (see Table 16). The greatest number of shrubs reach their highest frequencies here (see Figs. 11 and 12). Shrub frequencies, with the exception of Rosa woodsii and Cornus stolonifera, are lower in the open floodplains.

Composition of the Floodplain Stands: Stands 7, 8, 9, 10, 21, 22, and 24, found in the more open floodplains, have the highest importance values for P. trichocarpa (see Fig. 2). Tree densities range from 287 to 26 trees per acre. The younger stands developing on islands and newly formed sand deposits or floodplains are the densest stands viz., stands 7, 8, 10 and 21. The stands, supporting larger trees and situated on more stabilized land forms, have lower tree densities (see Table 11).

Ponderosa pine, Douglas Fir and Lodgepole pine also occur as scattered individuals in these stands (see Fig. 2). The importance value for *P. trichocarpa* ranged from 300 to 262.4, but sapling densities for the floodplain stands were lower than in any other group in the ordination. These data, however, do come from stands with the majority of the trees at least in the 4-10 inch class. Stands which are just invading newly formed sandbars have extremely high densities of saplings, just as alder swamps found in low areas of the river systems may have extremely high sapling densities. However, the sample in this study was from more mature forests.

P. trichocarpa was the major sapling (see Fig. 7) and *Salix alba*, *Alnus incana*, *Betula occidentalis*, *Pinus contorta*, *Juniperus scopulorum*, *Juniper communis* and *Crataegus douglasii* were represented by low densities.

Seedlings of *Pinus ponderosa* and *P. trichocarpa* were common in these types of stands. The seedlings of ponderosa were usually restricted to the more stable areas, and those areas less subject to inundation. *P. trichocarpa* seedlings were common in the earlier successional stages where mineral soil was available for germination. In those stands that were covered by a well developed herb layer of grasses the seedlings were absent *viz*., stands 9, 22, and 24 (see Table 15). Some sampling error is introduced in the data from Table 17. Stands 7 and 8, which are similar to some earlier stages in the floodplain succession, were sampled soon after the floodwaters subsided. The seedlings at this time were less evident, therefore they probably received a lower frequency than if they had been sampled later in July.

The frequencies of twenty of the most common herbs to this group are given in Table 15. The most common of these are Agropyron repens, Bromus inermus, Poa compressa, Poa pratensis, Poa palustris, Calamagrostis canadensis, Cirsium arvense, Solidago canadensis, Achillea millefolium, Centurea maculosa and Tanacetum vulgare (see Fig. 13). In the older stands such as 9, 22, and 24 an almost savanah appearance is given by a solid and continuous layer of Poa spp. and Agropyron spp. Observations indicate the drier areas are dominated by Agropyron spp. and the moister by Poa spp. These are the kind of stands where P. trichocarpa usually reproduces by root sprouts and these seedlings reach low frequencies (see Table 15).

The shrubs in the floodplains are represented primarily by Rosa woodsii, Cornus stolonifera, and Symphoricarpus albus; however, in the less disturbed spots Philadelphus lewisii, Rubus idaeus, Amelanchier alnifolia, Ribes setosum and R. lacustre are present. Salix exigua, Salix bebbiana, and Salix scouleriana in some cases form extensive stands on the edges of the bottomland forests, but seldom are important as layers within the forest canopy.

Composition of High Elevational Stands: Stands 12, 13, 14, 15 and 21 all occur at higher elevations from 4,300 to 4,600 feet above sea level in the Blackfoot and South Fork Valleys. The most striking differences lie in the sapling, shrub and herb layers; however, some tree characters are interesting also.

Picea engelmanni was first dominant in stand 14. This species obtains its second highest importance value in this stand. Stand 20 on the Middle Fork of the Flathead has the highest value for spruce.

The less disturbance, less severe climate, lower altitude, and more open valley in the Middle Fork near Kalispell may have been reasons permitting saplings such as _Prunus virginiana_ to thrive there and not in stand 14. This presence of some of the lowland species in stand 20 pulled it closer to the less disturbed tributary stands floristically, despite its similarity to 14 in regards to _P. engelmanni_. Stand 15 contains _P. englemanni_ as second dominant.

The floodplain stand in the South Fork Valley (stand 21) is grouped at the farthest end of the Y- axis indicating its similarity to the floodplains in the other parts of western Montana (see Fig. 3). However, its lower value on the X- axis demonstrates its relationship to the higher elevational stands.

Twenty-five of those plants most common to the high elevational stands are given in Table 16. _Arnica chamisonis_, _Aster hesperius_, _Erigeron speciosus_, _Prenanthes sagittata_, _Senecio pauperculus_, _Sedum stenopetalum_, _Carex hassei_, _Carex veridula_, _Calamagrostis inexpansa_, _Danthonia intermedia_, _Deschampsia caespitosa_, _Koeleria cristata_, _Muhlenbergia richardsonis_, _Bromus marginatus_, _Sisyrenchium sarmentosum_, _Hedysarum sulphurescens_, _Allium schoenoprasum_, _Anemone multifolia_, _Anemone parviflora_, _Dryas drummondii_ were only collected in these stands (see Fig. 14).

Eleagnus comutata, _Shepherdia argentea_, _Potentilla fruiticosa_ were the most prevalent shrubs in these stands. _Potentilla fruiticosa_ was only found in the South Fork stands (see Table 16).

Successional Features: Some of the aspects that are involved in the development of the land types along river systems in western Montana and elsewhere have already been discussed in the section that deals with river dynamics. It should be clear, however, that any interpretation of the successional trends in the river systems is a complex one. This is illustrated by such authors as Jeffrey (1963) who has shown that the succession on the Liard River is more of a matrix than a stepwise progression. This involves what has been termed by Raup (1964) for upland sites as an "open" type of forest development. In the bottomland environment, this concept is emphasized because of the relatively high rate of change in the forest over a relatively short period of time, due to the constant and frequent environmental disturbances which impinge on the bottomland forests by the rivers.

The various sites that might be studied in interpreting forest succession in the lowlands would include point bars, marshes, shrub thickets and the oxbow lakes which surround the main river channel.

The present study was concerned with the mature forests that occur along the lowlands in western Montana; little sampling was undertaken in those early successional stages that often surround the main river channels. Only two of the earlier successional stages were sampled. These were both sampled by one meter quadrats placed at twenty randomly selected points. It is impossible with this small a sample to even attempt to show the successional matrix which is believed to exist; however, the data from these two stands will be given.

Alnus incana and *Salix alba* are frequently encountered as a part of the more mature forests. This community type is characterized by the presence of a buried organic layer and numerous sand and silt layers overlaying one another. The dominant shrub in one stand is

Salix exigua with scattered individuals of P. trichocarpa that are invading the stand. Understory species that are present in the stand include Poa pratensis, Poa compressa, Poa palustris, Agropyron repens, Equisetum fluviatile, Equisetum arvense, Calamogrostis canadensis, Mentha arvensis, Centurea maculosa, Taraxicum officionale, and Salix alba. These species are all present with a frequency of 20% or greater.

The other stand studied that represents this early stage of development was on the lower part of the Clark's Fork between St. Regis and Paradise. This stand is characterized edaphically by the presence of numerous boulders that were covered by a thin layer of coarse sand. This stand appears to be very xeric. The water holding capacity of the A layer is 40% and that of the B layer, 80%. This is the lowest total water holding capacity of any of the stands that were sampled. There are no buried profiles evident in this stand as there are in the stand that supported a higher percent of Salix as well as the various grasses that have been listed above. This stand is situated on a lower level, and is subject to longer periods of inundation. Stand 11 is found on a higher bank at the edge of a young, developing black cottonwood forest. The understory plants that reach a frequency of greater than 20% are Coreopsis atkinsoniana, Aster laevis, Festuca rubra, Equisetum arvense, and Artemesia lindleyana. Equisetum arvense achieves a frequency value considerably higher than in the stand that appears to be in a more advanced stage of development with a higher percent of grasses.

Equisetum arvense is an early invader in those bottomland areas of western Montana where poor soil development, characterized by scattered boulders, is present. As the soil layer develops, Equisetum seems to decline in abundance and other grasses appear to replace it. Salix exigua also forms denser stands where the soil is deeper and buried profiles are present. Salix seedlings reach a quadrat frequency of 10% in stand 11, and are absent in stand 17.

The type of species composition that is represented in stands 11 and 17 is typical of communities that are found on the Clark's Fork and the Bitterroot Rivers. This is particularly true of the representation of the grass species in the willow thickets, and the higher frequency values for horsetail in those areas that have a shallow layer of the coarse sand over boulders.

The results that are given by Orloci (1963) have already been reviewed, but it is of interest to note that in British Columbia, on the Squamish River, Equisetum plays an important role in the early establishment of plants on the newly exposed soil that is similar to the type found in western Montana. Orloci describes a decline in the abundance of Equisetum as the site's soil texture, depth and the number of overflow days change.

DISCUSSION AND CONCLUSIONS

General: The purpose of the study was to sample as many different types of bottomland stands in western Montana as possible. The results given in the discussion of tree dominants and of the ordination, demonstrate the phytosociological variability found in the forests of the different river systems in western Montana. Variation occurs in composition, density, dominance and distribution of the tree and sapling species. Understory shrubs and herbs also demonstrate wide variability in the composition and their distribution. Statements such as the broad leafed deciduous element being "conspicuous" everywhere along the bottomlands of western Montana are misleading, because they infer a similarity between the bottomland stands. This is shown not to be completely true for the trees, shrubs, and herbs. The only real similarity is that *P. trichocarpa* is present in almost every bottomland stand. Its associates, however, vary widely. "Black cottonwood has the greatest altitudinal range in any given latitude of any given tree on the North American continent" (Balfour, 1943; pp. 50-53). This characteristic impresses an unrealistic uniformity on all bottomland stands because the apparent dominance of *P. trichocarpa* and its species physiognomy makes all of these stands appear similar. However, these stands differ and the difference seems to be caused by irregularities in the geography, topography, and climate of the stands.

Perhaps the most similar of the bottomland stands are the early successional stages of the wider floodplains. In these stands *P. trichocarpa* is usually the only tree and it obtains importance values of 300 percent. In later successional stages the land becomes more stable. A subsequent increase in the organic layer of the soils and a deepening of the soils then follows. The montane forests of the area begin to invade the bottomlands and P. trichocarpa gradually declines in importance value. Pinus ponderosa, Picea engelmanni, Pseudotsuga menziesii, Abies grandis, Pinus contorta, Thuja plicata, Populus tremuloides and other members of the higher or less disturbed sites soon become established in the understory of the stands. In many cases these trees grow to the dominant role in the communities as the river system migrates away from these stands and makes it possible for greater environmental stability. Whether a stand is invaded by Pinus ponderosa or by one of the other species is probably most dependent on the geographic and topographic position of the stand. Those stands that are located in the more open valleys of the Bitterroot, Clark's Fork, and Flathead Rivers as well as the stands that are located in the tributaries, if they are adjacent to stands of Pinus ponderosa, are generally invaded by Pinus ponderosa. The higher stands and those stands at higher latitudes that appear to be in cooler, moister areas are often invaded by Picea engelmanni and Abies grandis. The stands that are in areas of higher precipitation where Thuja plicata is one of the forest dominants are eventually dominated by this species. The stands that are located in areas adjoining forests of Pseudotsuga menziesii are invaded by this species. Therefore, it is evident, that the later stages of the tree composition in the bottomlands are largely dependent on the geographic, climatic and the topographic position of the stand. Kirkwood (1922) also states that these are the factors that determine the distribution of the forests in western Montana.

Geographic Forest Regions of Western Montana: Kirkwood (1922), in a discussion of the different forests that occur in the northern Rockies, divides the area into fifteen different sections. These are divisions based on the topography and climate. The vegetation in these different areas appears to be a result of the environmental conditions that are present. The stands that were sampled in this present bottomland study were in four of these sections. The first that Kirkwood delimits, where bottomland stands were sampled, extends in Montana into the lower valley of the Clark's Fork to the summits of the Cabinet Mountains and Evaro Pass. The most predominant trees that grow at lower elevations in the montane forests of this region, according to Kirkwood, are: *Pinus ponderosa*, *Larix occidentalis* and *Pseudotsuga menziesii*. Other species that make up a smaller per cent in this region are *Thuja plicata*, *Tsuga heterophylla* and *Abies grandis*. Stand 23, which was the only tributary stand that was sampled in this region, contains *Thuja plicata*, *Larix occidentalis*, *Pseudotsuga menziesii*, and *Abies grandis*. The stands 8, 9, and 22 which occur in open floodplains of this region contain *Pinus ponderosa* and *Pseudotsuga menziesii* in the later, more well established areas which also contain black cottonwood.

The second section in which bottomland stands were sampled was in the drainages of the North, Middle and the South Forks of the Flathead River. Stands 12, 13, 14, 18, 19, 20, 21, and 44 occur in this section. The most common montane species at lower elevations are: *Larix occidentalis*, *Picea engelmanni*, and *Pseudotsuga menziesii*. Those species with a lower frequency in this area are *Pinus ponderosa*, *Pinus monticola*, *Pinus albicaulis*, *Tsuga heterophylla*, and *Abies grandis* (Kirkwood, 1922).

Larix occidentalis, Abies albicaulis and Pinus monticola were the only trees of this group that were not found in the bottomland stands. It is interesting to note that although Kirkwood states that in this region the ponderosa pine is a minor species in the overall composition of the forests, this species obtains one of its highest relative importance values in this region for all of the ponderosa stands that were sampled. Pinus ponderosa attains relatively high importance in some of the more open, drier valleys of this region. Pseudotsuga menziesii, Picea engelmanni, and Thuja plicata obtain higher importance in the narrower valleys, or in the cooler, moister valleys. The occurrence of spruce in the wider bottomlands of the upper Flathead Valley near Kalispell appears not to agree with this statement. This is the widest valley that was sampled in the study, and therefore, one would believe that drying winds would lessen the probability of the survival of this species in this environment. In the case of spruce, however, it is possible that cooler temperature is more limiting than moisture. This is a cooler valley, probably due to the drainage of the air from the surrounding mountains (see Table 6).

Kirkwood's third region where some stands were sampled was in the Bitterroot Valley. Stands 3, 4, 5, 6, 7, and 24 were located in this area. Pinus contorta, Pinus ponderosa, and Pseudotsuga menziesii are the most common trees of this forest region. Picea engelmanni, Larix occidentalis, Abies grandis and Thuja plicata are lower in abundance (Kirkwood, 1922). Pinus contorta and Thuja plicata were the only species that were not recorded in at least one of the bottomland stands sampled in this area. The species of this valley, in contrast to those species found in the more northern valleys, are more adapted to the drier conditions (Kirkwood, 1922). In the later stages of succession Pinus ponderosa is the most important species in the wider and drier floodplains. In higher, moister and cooler valleys and in those areas where the streams are close to the montane forests the chief associates with P. trichocarpa are: Abies grandis and Picea engelmanni, and in the slightly drier sites, Pseudotsuga menziesii. It has already been stated that this valley is in the shadow of the Bitterroot Mountains. Picea engelmanni does not occur in the wider portions of the Bitterroot Valley in a comparable elevation to that of the Flathead Valley. It is confined to the narrower valleys of the tributaries, despite the fact that this valley in its lower portions reaches a similar elevation to that of the Flathead Valley. The temperatures are higher and the moisture is lower in the Bitterroot valley at comparable elevations to the Flathead.

The fourth section is the region of the upper Clark's Fork and the Blackfoot River. At lower elevations Pseudotsuga menziesii, Pinus ponderosa, Picea engelmanni, Abies lasiocarpa, and Pinus contorta compose the major and minor parts of the forest (Kirkwood, 1922). Pinus contorta and Abies lasiocarpa were the only ones that did not occur in any of the sampled bottomland stands. Stands 1, 2, 10, and 16 were located in this region. Pinus ponderosa and Picea engelmanni are the most common coniferous associates of P. trichocarpa in this region. The former is again associated with the bottomland in the drier areas around the region of Missoula. This is in stand 1 where there is an even distribution of Pinus ponderosa becoming established under the older P. trichocarpa. This is in a region of an ancient floodplain that is no longer inundated by the river even in the years of highest water levels. _Picea engelmanni_ is found in the higher Blackfoot Valley where the moisture is higher and the temperatures are cooler than the lower, more southerly Missoula Valley. In the higher portions of the tributaries of this region, where the valleys are narrower and the temperatures are also presumably cooler, spruce is present. It gradually becomes less noticeable along the tributary stands close to the valley floor. _Pinus ponderosa_ becomes more prevalent in the lower areas. This is seen in stands 1 and 2. Both _Pinus ponderosa_ and _Pseudotsuga menziesii_ are common in the main bottomlands of the larger rivers of this region, but _Pseudotsuga menziesii_ reaches its greatest development in the areas where the river approaches the montane forest.

Environmental Gradients and Succession in the Physiographic Regions: The two dimensional vegetational ordination that was constructed with the tree data separates the bottomland stands into three physiographic regions. These regions are proposed to be the result of environmental gradients that cause different vegetational communities to develop. Slight differences between compositional characters in the stands are thought to be the result of differences in the position along the environmental gradient for that particular stand.

The two dimensional ordination of the cottonwood stands found in western Montana demonstrates the different floristic composition of those forests found along less disturbed tributary rivers, higher elevational rivers and lower elevational rivers in the broader valleys with the more active floodplains.

The strongest environmental factor that apparently governs the floristics in the bottomland stands is the geographic location and the climate and topography of this location. These features probably control other gradients such as humidity, temperature, and number of overflow days, or degree of disturbance, which would affect soil moisture, soil depth and soil texture.

Topography, aside from geographic position, is the strongest environmental gradient separating the bottomland stands. "Topography affects vegetation indirectly by modifying other factors of the environment. It has nevertheless a significant influence upon all plant communities .... irregularities in topography produce light, temperature, and moisture conditions that differ greatly between north and south slopes or ridges and depressions" (Oosting, 1956; p. 204). The narrower valley stands in both the tree ordination and the understory ordination separated themselves from the more open floodplains floristically (see Fig. 3). The environmental conditions that might be affected by the difference in the topography between the tributary and the floodplain stands are probably those suggested by Oosting (1956) as well as some of those illustrated by Orloci (1964). These would include humidity, temperature and the number of overflow days, the soil texture, soil depth, and soil moisture. In the environmental continuum constructed by Orloci, differences in topography or relief were eliminated, for Orloci was working in one river system. Variation in the stands could therefore be attributed to one of the other environmental factors, such as overflow days, soil texture, or soil depth.

In the study on the bottomlands in western Montana, geographic or topographic variables were not eliminated. The stands differed in the geography, topography, number of overflow days, soil texture, soil depth, and the age of the stands. From this study, therefore, one conclusion can be drawn: the strongest environmental factor affecting the bottomland hardwood composition is first the geographic position and second the relief or the topography.

Certain plants do not extend from the Canadian border to the southern Idaho-Montana border. Therefore, one bottomland community composition found in Glacier County may not occur further south because certain plants are geographically restricted in their range to certain parts of western Montana. A tributary stand in one portion of the state may not be expected to be composed of the same species as a stand in another part of the state. Differences in the climate of the area may cause the variation in the vegetation. This infers that there are different successional stages on the river systems of western Montana depending on the geographic position and the topography. Further research on the different river systems, with an emphasis on comparing the successional patterns in these and measuring microenvironmental factors, would enlighten the understanding of what the environmental differences were that caused the variation in bottomland succession, and subsequently in the older forests in the different geographic regions. If a sufficient number of successional stands of the different topographical areas would have been sampled in the study, successional trends could have been shown, but from the variation in the composition of the older stands that were sampled in the different river systems, it is apparent that different steps in succession occur in the different geographic and topographic regions. The species that occur in the later stages of succession in these different areas would depend on the species that are present in the montane forests of the region. The presence or absence of a particular species in a certain area is dependent on the topography and the climate of a particular region (Kirkwood, 1922).

The mention of the successional interpretation of the bottomland stands affords another interesting facet for discussion.

"Units of vast extent and great permanence, are termed climaxes or formations; they are the product of climate and are controlled by it. Each formation is the highest type of vegetation possible under its particular climate, and this relation makes the term climax especially significant, as it is derived from the same root as climate" (Weaver and Clements, 1929; p. 421). The attainment of the climax involves progression toward habitat stability from pioneers to a stable community. These climaxes remain until slow physiographic or climatic changes alter them. One of the exceptions to the climax vegetation might be the bottomland forests; these are more of an "open system" (Raup, 1964; p. 23). Raup proposes this theory with regard to an upland site but some of his ideas are applicable to the bottomlands. He states that in the forest, the species of the area "is a function of the ... ecotypes that were available to it as it emerged from the last major disturbance of its habitat. Our understanding of it will depend upon our knowledge and interpretation of the history, geographic distribution and tolerance of the species, projected against site complexes in which we can see some order along gradients in space at points in time" (Raup, 1964; p. 23).

Hypothetical stands can be sited as the stages in succession in the open floodplain river system; however, all of the stands do not start at the same place in succession. Some may start at the Equisetum boulder stage in a particular area, but another area may start with Carex and a buried profile of sands and silts. Whatever their starting place in succession, they are dependent on time for the stage that they finally reach. A hypothetical case illustrates this point.

The forest that theoretically is "climax" is ponderosa pine in the bottomlands of the wider Bitterroot Valley in the region near Missoula. The earliest stages in succession of the bottomlands of this region are often dominated by Equisetum spp., Salix spp., and Populus trichocarpa. The P. trichocarpa occurs in dense sapling stands and later develops into more open stands with a dominantly grass understory. The reproduction of P. trichocarpa in this later type of stand is mostly restricted to vegetative root sprouts while in the earlier it is sexual. This is apparently due to the inability of P. trichocarpa saplings to compete with the denser understory of grasses. The site then becomes more stable as the river migrates away from the stand and the number of overflow days declines. Pinus ponderosa then may invade the area and the saplings become established as trees. As the site becomes drier and the river migrates further from the stands the availability of water declines and the predominantly cottonwood stands now become predominantly ponderosa. Occasional oxbows in the area still support cottonwood along the periphery, as well as some of the shrubs that are characteristic of the moister sites: Alnus incana and Cornus stolonifera. Populus tremuloides also may be common on the margins of the oxbow lakes. The main portion of the forest, however, is Pinus ponderosa, and this might be considered to be the climax for this region. The river, however, now may begin to migrate back toward the stand and soon, with the spring high water, the evidences of the migration of the river toward the stand can be seen by the ponderosa that are undercut by the migrating river. The succession now may begin again.

It is illustrated that the theoretical "climax" was only attained for a relatively short time. This is a hypothetical argument, but there is good evidence that a constant disturbance in the river systems is present. This impresses an uncertainty on the prediction of the successional trends of a certain river forest within a certain time period. Differences in the starting points of the successional stages and differences in the length of time that elapses between disturbances will probably cause variations to occur in the community composition. The prediction of successional stages of a particular forest therefore is made more difficult by these factors. However, hypothetical predictions can be made by examining different stands along one river system. The different forests found along a particular river can be correlated with environmental factors. However, variations in river action can change the path of succession of a given stand.

The disclimax condition that is maintained by the river is beneficial for maintaining cottonwood in the bottomlands of western Montana. Data taken from the sampling of the tributary stands, and older floodplain stands, indicate that as the stands become older and are invaded by either surrounding vegetation or herbs, cottonwood density declines.

One characteristic that is common to the cottonwood stands is that they are usually composed of one tree size. This tree size usually corresponds to the relatively short time when the stand is first established. The density at early stages of cottonwood development is higher than later. After first establishment of the community there is little survival or establishment of new trees after this time in a homogeneous, undisturbed stand.

The succession in the tributary stands appears to be more predictable, for the rivers in these stands usually are not subject to as great lateral migration. These stands are more subject to disturbance factors similar to those found in the montane forests.

Though the tree sizes in the tributary stands that were sampled are generally larger than those found in the floodplain stands, this is caused by sampling bias. Large trees in the wider floodplains do occur, but these are found in the older stands that are away from the active floodplain. It should be recalled that these stands were eliminated from the sample because of the disturbance from grazing. In the tributary stands the older stands that are being invaded by conifers again have generally one size class of cottonwoods.

Similar to what has been described for the floodplains, the older tributary forests being invaded by conifers are composed of mainly one tree size class. This indicates that at one time these stands were similar to the stands found on the floodplains. However, the invasion of the conifer and the higher density of arborescent trees, shrubs and herbs, and lack of inundation, probably cause faster rate in the aggregation of the litter layer. This may be a major factor influencing tributary herb growth. The faster aggradation of litter also probably makes the environment less favorable for the establishment of the cottonwood seedlings. This species needs bare soil, sun and few competitors in order to survive as a seedling and sapling. These tributary stands will therefore probably succeed to a mostly coniferous forest when the cottonwood trees that first became established die. A few cottonwoods may survive on the edge of the creeks in more of a ravine situation, surrounded by a coniferous forest. The trees that survive in this site may be composed of a more varied size distribution. Saplings of cottonwood may become established in mineral soil at the edge of the creek.

The increased use of some of the tributary valleys for house building in the regions of greater urbanization may increase the rate of succession toward a higher coniferous element in these minor tributary stands, for the clearing of the land will probably have a drying effect on the stands adjacent to the clearing. Also the prevention of lateral river migration by the use of dikes and retaining walls will probably reduce the cottonwood in the tributary rivers especially.

It is doubted if the understory vegetation of the tributary stands will develop into one similar to that of the major floodplains, because of the large difference in soil types between the two types and the greater litter that is provided by the deciduous shrubs. However, in some tributary environments, where the creek has formed benches, these areas may develop into ponderosa savanahs similar to those found where the larger rivers have left ponderosa forests on the higher benches.

Restatement of the Species Behavior and the Environmental Gradients: The quartile data on the ordination demonstrate that in the tributary stands and in the more protected areas of moister, cooler, and less disturbed environments, *Abies grandis*, *Thuja plicata*, and *Tsuga heterophylla* were the most geographically restricted. *Picea engelmanni* in the warmer and drier Bitterroot Valley is confined to the moister and probably cooler ravines and tributary stands. This species, however, in the cooler portions of the Blackfoot and the Flathead Valleys occurs along the main floodplains. Elevation does not appear to be the limiting factor for the presence of this species in the bottomlands, but instead, moisture and temperature may be more important. Spruce does not occur at similar elevations in the Bitterroot and Flathead valleys. In the Bitterroot Valley spruce is restricted to the narrower valleys. *Pseudotsuga menziesii* and *Pinus ponderosa* are more ubiquitous than the other coniferous species and they occur in the open floodplains and in the narrower tributaries with cottonwood.

The understory plants that occur in the stands are also characteristic of the different physiographic types. In the shadier, moister, and less disturbed tributary stands *Osmorhiza chilensis*, *Heracleum lantanum*, *Disporum trachycarpum*, *Actea rubra*, *Circaea alpina*, *Galium triflorum*, *Pyrola asarifolia*, *Polypodium hesperium*, *Ranunculus uncinatus* and *Aytherium felix-foemina* have the highest fidelity. In the sunnier, drier, disturbed, more open floodplain stands *Poa pratensis* *Poa compressa*, *Agropyron repens*, *Poa palustris* and *Elymus glaucus* have the highest frequency. Some of these species also obtain high frequencies in the tributary stands where openings in the canopy occur. These openings are in some instances caused by blow downs and old fires. In the stands on the South Fork of the Flathead River Aster foliaceus, Gaillardia aristata, Solidago missouriensis, Arctostaphyllos uva-ursi, Deschampsia caespitosa, Koeleria cristata, Allium schoenoprasum, Dryas drummondii, and Antennaria rosea are the most common species. It is noted that due to the extreme erosion in these stands much of the understory is destroyed.

The variation in the composition of the bottomland stands at first glance appears to present a problem in the interpretation of species behavior and successional patterns in the forest stands when explained by associations. However, in different geographic regions of western Montana where the surrounding vegetation is different, due to differences in the climate and topography, there appear to be variations in the successional progressions of the plant communities.

In any particular geographic region the most obvious environmental gradients for the cottonwood stands appear to be controlled by topography. Tributary stands and narrow valley riparian sites seem to be related and open floodplain sites are related phytosociologically. In different geographic locations, the most similar stands are the open floodplains and the tributaries exhibit greater compositional variability. However, differences in the composition of these stands within the same physiographic group is probably caused by the different position of these stands along an environmental gradient. The most obvious gradient shown by the vegetative continuum is controlled by topography at a particular geographic location.

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APPENDIX

TABLE I - GEOGRAPHICAL, LATITUDINAL, ELEVATIONAL, AND ENVIRONMENTAL SITE OF BOTTOMLAND FORESTS SAMPLED

Stand N.	Latitude	Elevation	Exact Location (River System, County, Etc.)
1	46° 55'	4000	Rattlesnake Creek, Missoula Co., vicinity of Rattlesnake School, near Missoula.
2	46° 55'	4000	Rattlesnake Creek, Missoula Co., north of Papoose Ranch, near Missoula.
3	46° 45'	3200	Lolo Creek, Missoula Co., 2 mi. up creek, on south side of creek.
4	46° 45'	3200	Lolo Creek, Missoula Co., 2 mi. up creek, on north side.
5	46° 36'	4000	Sweeney Creek, Ravalli Co., 1/4 mi. west of U.S. 93.
6	46° 34'	4000	Bass Creek, Ravalli Co., Waters Camp Ground.
7	46° 33'	3600	Bitterroot River, Ravalli Co., island just below Bass Creek.
8	46° 52'	3200	Clark Fork River, Missoula Co., Orchard Homes Area, Island opposite Short Street.
9	46° 55'	3200	Clark Fork River, Missoula Co., island by Deep Creek Bridge.
10	46° 49'	3200	Bitterroot River, Missoula Co., U. of M. Arboretum.
12	47° 34'	4660	South Fork of Flathead River, Flathead Co., Holbrook Creek Crossing, Bob Marshall Wilderness.
13	47° 34'	4660	South Fork of Flathead River, Flathead Co., Holbrook Crossing, Bob Marshall Wilderness.
14	47° 37'	4660	South Fork of Flathead River, Flathead Co., at Salmon Forks, Bob Marshall Wilderness.

TABLE I (CONTINUED)

Stand N.	Latitude	Elevation	Exact Location (River System, County, Etc.)
15	46° 58'	4300	Blackfoot River, Powell Co., at corner north of Helmsville Road, cut-off Rt. 20, 63 mi. from Missoula.
16	46° 58'	4300	Blackfoot River, Powell Co., 1 mi. east of Helmsville Crossing, Rt. 20 west of Kiwanis Picnic Area.
18	48° 6'	2900	Oxbow Lake, Flathead Co. Road north of Somers cut-off. 2 mi. west of Rt. 2.
19	48° 6'	3000	Oxbow Lake, Flathead Co., near Flathead River, 1 mi. west of Mcvinegar's Slough.
20	48° 5'	3000	Flathead River, Flathead Co. west of bridge over Flathead on main road to Kalispell.
21	47° 35'	4660	S. Fork Flathead River, Flathead Co., Bob Marshall Wilderness, north side Murphy Flats.
22	47° 2'	3200	Clark Fork River, Missoula Co., 9 mi. area west of Frenchtown.
23	47° 17'	2537	Clark Fork River, Mineral Co., 15 mi. west of St. Regis on south side of highway.
24	46° 33'	3600	Bitterroot River, Ravalli Co., 2 mi. south of Bass Creek, turn off on Rt. 93.
44	48° 34'	3250-3300	Lake McDonald, Glacier Co., Glacier National Park, east side of road, south of Snyder Creek.

TABLE 2. ILLUSTRATION OF BURIED ORGANIC LAYERS IN MORE DISTURBED SITES

Stand	Location	% Organic Matter in first layer	% Organic Matter in second layer
23	t	11.94	4.93
1	t	31.40	16.70
2	t	15.50	11.80
5	t	19.70	10.80
6	t	23.90	12.10
18*	o	21.17	45.78
3	t	9.20	8.61
44	t	-----	-----
4	t	17.70	15.50
9	f	-----	-----
10*	f	00.90	2.23
24	f	17.29	2.84
20*	f	4.80	13.90
7	f	7.28	2.49
19*	o	9.61	20.18
22	f	18.08	10.62
8	f	10.35	5.36
15*	f	9.18	9.73
21	f	-----	-----
12*	f	2.52	3.73
13*	f	6.47	12.13
14	f	9.38	4.39

t = Tributary stand
o = Oxbow stand
f = Floodplain stand
* = Indicates lower % organic matter in first soil layer

TABLE 3. COMPARISON OF STREAMFLOW FOR THE YEARS 1955-1964 (MONTANA POWER, 1965)

Station & River System	Date of Highest River Flow	Streamflow (cubic feet/second)
Milltown Dam Clark's Fork River	13 June, 1955	11,190
	2 June, 1956	16,010
	1 June, 1957	12,260
	12 June, 1958	12,620
	7 June, 1959	18,560
	4 June, 1960	10,620
	1 June, 1961	14,610
	16 June, 1962	12,900
	5 June, 1963	9,970
	10 June, 1964	28,000

TABLE 4. THE HIGH WATER DATES OF THREE RIVERS IN WESTERN MONTANA (MONTANA POWER, 1965)

Station & River System	Date of Highest River Flow	Streamflow (cubic feet/second)
Clark's Fork River-Milltown	10 June	28,000
Flathead River Kerr Dam	12 June	63,450
Clark's Fork River-Thompson Falls, Montana	11 June	125,700

TABLE 5. ILLUSTRATION OF PHYTOGEOGRAPHICAL ORIGIN FOR SOME OF THE SPECIES ENCOUNTERED IN BOTTOMLAND FORESTS

Species	Stands of Occurrence	Possible Origin		Source
		North-ern	For-est	
Juniper communis	8,12,13,21	North-ern	For-est	Kirkwood (1922)
Populus tremuloides	2,5,15,19,18,16	"	"	"
Betula papyrifera	18	"	"	"
Alnus incana	1-6,8,9,11,12-14, 23	"	"	"
Ribes lacustre	1-3,7	"	"	"
Ribes hudsonianum	1-4	"	"	"
Shepherdia argentea	12-16	"	"	"
Rhamnus alnifolia	5,6,13,20	"	"	"
Cornus stolonifera	1-10,12-16,18-20, 22,24	"	"	"
Arctostaphylos uva-ursi	6,8,12-14,21	"	"	"
Deschampsia caespitosa	12,13,14,21	"	"	Daubenmire (1952)
Chrysopsis villosa	8,13,15,21			"
Pinus contorta	8,12,14	W or NW		Kirkwood (1922)
Pseudotsuga menziesii	3,5,8,12,13,44	" " "		"
Abies grandis	6	" " "		"
Betula occidentalis	1,2,3,5,6,8,15,16, 19,23	" " "		"
Philadelphus lewisii	1,2,3,6,7,23	" " "		"
Rubus parviflorus	1,2,6,23	" " "		"
Populus trichocarpa	All Stands	" " "		"
Amelanchier alnifolia	1-8,12,15,18,20,21, 23,24	" " "		"
Crataegus douglasii	1-4,7,8,18,20,21,23, 24	" " "		"
Sorbus scopulina	1-3,6	" " "		"
Holodiscus discolor	1,2,5,6	" " "		Benson (1957)

TABLE 6. CLIMATIC, TOPOGRAPHIC, AND ORDINATIONAL FEATURES OF BOTTOMLAND FORESTS SAMPLED

Stand No.	Point on X-axis	Elevation	Approx. Width of Valley	Location	Mean Annual Pcpt.	Mean July Temp.
23	87.0	2537	.5-	trib.	15.5	66.6
1	72.9	4000	.5-1	trib.	14.0	67.6
2	67.0	4000	.5-1	trib.	14.0	67.6
5	66.0	4000	1+	trib.	12.2	66.3
6	61.7	4000	.5-	trib.	12.2	66.3
18	59.3	2900	1+	oxbow	14.5	64.1
3	58.4	3200	.5-1	trib.	14.0	67.6
4	53.4	3300	.5-1	trib.	20.6	65.8
4	48.4	3200	.5-1	trib.	14.0	67.6
9	48.1	3200	1+	flood.	14.0	67.6
10	43.5	3200	1+	flood.	14.0	67.6
24	40.9	3600	1+	flood.	14.0	67.6
20	38.4	3000	1+	flood.	14.5	64.1
7	38.2	3600	1+	flood.	12.2	66.3
19	38.1	3000	1+	oxbow	14.5	64.1
22	36.4	3200	1+	flood.	14.0	67.6
8	34.7	3200	1+	flood.	14.0	67.6
15	26.1	4300	.5-1	flood.	17.4	61.8
21	24.8	4660	1+	flood.	18-20	62
12	22.7	4660	1+	flood.	18-20	62
13	20.7	4660	1+	flood.	18-20	62
14	0.0	4660	1+	flood.	18-20	62

TABLE 7. TREE DOMINANTS IN BOTTOMLAND FORESTS SAMPLES

Stand No.	First Dom.	Second Dom.	Third Dom.	Fourth Dom.
21	cottonwood	*	*	*
22	cottonwood	*	*	*
9	cottonwood	ponderosa	*	*
7	cottonwood	ponderosa	*	*
10	cottonwood	ponderosa	*	*
24	cottonwood	ponderosa	willow	*
13	cottonwood	ponderosa	fir	juniper (r.m.)
2	cottonwood	ponderosa	maple	aspen
1	cottonwood	ponderosa	maple	birch
3	cottonwood	alder	fir	ponderosa
4	cottonwood	alder	larch	birch-juniper (rb)
8	cottonwood	alder	*	*
5	cottonwood	birch	alder	aspen
23	cottonwood	birch	cedar	maple
15	cottonwood	spruce	aspen	ponderosa
12	cottonwood	lodgepole	fir	*
20	spruce	cottonwood	cherry	*
14	spruce	cottonwood	lodgepole	fir
19	aspen	cottonwood	birch	*
18	aspen	cottonwood	*	*
16	aspen	ponderosa	fir	*
6	fir	birch	cottonwood	maple
44	cedar	cottonwood	fir	hemlock
	5 Types	11 Types	19 Types	20 Types

TABLE 8. MOST COMMON TREES, SAPLINGS, SHRUBS, AND HERBS FOUND IN BOTTOMLAND FOREST STANDS SAMPLED

Stand No.	Location	Trees 1 2 3 4	Saplings 1 2 3 4	Shrubs 1-2	Understory 1-2
21	F	co * * *	co * * *	RW-PF	J.confus-A.laevis
22	F	co * * *	co * * *	RW-CS	A.repens-A.canabinum-S.canadensis
9	F	co po* *	co bi al po	RW,CS, Sa	A.repens-P.compressa
7	F	co po* *	co ha wi po	RW-CS	A.repens-P.pratensis
10	F	co po* *	co po ch ha	RW-SA	P. compressa-P. pratensis
24	F	co po wi*	po ha wi ch	SA-AA	P.sp.-P.palustris
13	F	co po fi jr	jr al fi co	RW-CO	A.foliaceus T.hybridium
2	T	co po ma as	ha ch ma co	SA-RW	O.chilensis G.triflorum
1	T	co po ma bi	ma ch bi al	SA-Ri, RI	G.triflorum O.chilensis
3	T	co al fi po	al ch co ma	Sa-Pi	G.triflorum-O.chilensis
4	T	co al la-bi-jb	co al ch bi	Sa-Cs	G.triflorum-O.chilensis
8	F	co al * *	co al po fi	Sa-RW	C.maculosa-B.inermus
5	T	co bi al as	ch bi as al	Ri-Sa	T.officionale G.triflorum
23	T	co bi ce ma	ch ma bi ha	Sa-Rp	S.stellata-O.chilensis
12	F	co lo fi *	co lo fi al	Ra-PF, Sha	A.foliaceus-P.virginiana
15	F	co sp as po	co as ch sp	Sa-RW	G.triflorum-T.officionale

TABLE 8 (CONTINUED)

Stand No.	Location	Trees 1 2 3 4	Saplings 1 2 3 4	Shrubs 1-2	Understory 1-2
20	F	sp co ch *	ch ha sp co	Sa-RW	C.arvense-S.canadensis B.repens, E.fluviatile C.canadensis
14	F	sp co lo fi	jr co so al	RW-Sha	E.fluviatile-S.stellata
19	O	as co ha *	as co ha *	Co-RW, Sa	C.retrorsa + P.palustris
18	O	as co * *	co as ch ha	Sa-RW	S.stellata-T.officionale
16	F	as po fi *	as ch bi *	Sa-Ri	B.repens+ E.glaucus
6	T	ft bi co gf	gf bi al ma	Sa-Rp	A.cordifolia-S.stellata T.officionale
44	T	ce co fi he	ce he * *	Ri-Sa	S.stellata-G.aparine

F = Floodplain stand

T = Tributary stand

O = Oxbow stand

TABLE 9. KEY TO THE ABBREVIATIONS USED IN TABLES 7 and 8 FOR THE TREES, SAPLINGS, SHRUBS, AND UNDERSTORY HERBS

Category	Abbreviation	Common name	Scientific name
Trees and Saplings	co	Cottonwood	Populus trichocarpa
	po	Ponderosa Pine	Pinus ponderosa
	wi	Willow	Salix alba
	fi	Douglas Fir	Pseudotsuga menziesii
	jr	Rocky Mountain Juniper	Juniperus communis
	ma	Rocky Mountain Maple	Acer glabrum
	as	Trembling Aspen	Populus tremuloides
	bi	River Birch	Betula occidentalis
	al	Alder	Alnus incana
	jb	River Bottom Juniper	Juniperus scopulorum
	ce	West Red Cedar	Thuja plicata
	lo	Lodgepole Pine	Pinus contorta
	sp	Engelman Spruce	Picea engelmanni
	he	Western Hemlock	Tsuga heterophylla
	ha	Hawthorne	Crataegus douglasii
	ch	Choke Cherry	Prunus virginiana
	gf	Grand Fir	Abies grandis
Shrubs	rw	Wood's Rose	Rosa woodsii
	pf	Yellow Cinquefoil	Potentilla fruiticosa
	cs	Red-Osier Dogwood	Cornus stolonifera
	sa	Snowberry	Symphoricarpos albus
	aa	Serviceberry	Amelanchier alnifolia
	ri	Red Raspberry	Rubus idaeus

TABLE 9 (CONTINUED)

Category	Abbreviation	Common name	Scientific name
Shrubs	rl	Gooseberry	Ribes lacustre
	rp	Thimbleberry	Rubus parviflorus
	sha	Buffalo Berry	Shepherdia argentea
Understory Herbs			Juncus confusus
			Aster laevis
			Agropyron repens
			Apocynum canabinum
			Solidago canadensis
			Poa compressa
			Poa pratensis
			Poa sp.
			Poa palustris
			Aster foliaceus
			Trifolium hybridium
			Osmorhiza chilensis
			Galium triflorum
			Centaurea maculosa
			Bromus inermus
			Taraxacum officionale
			Smilacina stellata
			Fragaria virginiana
			Cirsium arvense
			Berberis repens

TABLE 9 (CONTINUED)

Category	Scientific name
Understory Herbs	Equisetum fluviatile
	Calamagrostis canadensis
	Carex retrorsa
	Elymus glaucus
	Arnica cordifolia
	Galium aparine

TABLE 10. LIST OF PLANTS FOUND IN BOTTOMLAND FOREST AND EARLY SUCCESSIONAL STANDS

Aceraceae
Acer glabrum Torr.

Apocynaceae
Apocynum cannabinum L. var. glaberrimum D.C.

Araliaceae
Aralia nudicaulis L.

Berberidaceae
Berberis repens Lindl.

Betulaceae
Alnus incana (L.) Moench.
Betula occidentalis Hook.
Betula papyrifera Marsh. var. occidentalis (Hook.) Sarg.

Boraginaceae
Lithospermum ruderale Dougl. ex. Lehm.
Merkensia paniculata (Ait.) G. Don
Myosotis laxa dehm.

Campanulaceae
Campanula rotundifolia L.

Caprifoliaceae
Sambucus coerulea Raf.
Symphoricarpus albus (L.) Blake.

Caryophyllaceae
Arenaria laterliflora L.
Arenaria obtusiloba (Rydb.) Tern.
Cerastium vulgatum L.
Silene cucabalis Wibel.
Silene menziesii Hook.
Stellaria crassifolia Ehrh.
Stellaria media (L.) Cyr.

Compositae
Achillea millefolium L.
Adenocaulon bicolor Hook.
Agoseris glauca Rof. var. glauca
Antennaria rosea Greene
Arnica chamissonis Less.
Arnica latifolia Bong. var. latifolia
Arnica cordifolia Hook.
Artemesia absintheum L.
Artemesia lindleyana Bess.

Artemesia ludoviciana Nutt. var. latiloba
Aster conspicuus Lindl.
Aster foliaceus Lindl.
Aster hesperius Gray.
Aster laevis L.
Aster modestus Lindl.
Centaurea maculosa Lam.
Chrysanthemum leucanthemum L. var. pinnatifidum Lec.
Chrysopsis villosa (Pursh) Nutt. ex. D.C. var. villosa
Circium arvense (L.) Scop.
Coreopsis atkinsoniana Dougl.
Erigeron speciosus (Lindl.) D.C.
Gaillardia aristata Pursh.
Helenium autumnale L.
Hieracium albiflorum Hook.
Hieracium umbellatum L.
Petasites sagittatus (Banks) Gray.
Prenanthes sagittata (Gray) A. Nels.
Senecio canus Hook.
Senecio indecorus Greene
Senecio pauperculus Michx. var. thomsoniensis (Greene)
Senecio pseudaureus Rydb.
Senecio serra Hook.
Senecio triangularis Hook.
Solidago canadensis L.
Solidago missouriensis Nutt. var. fasiculata
Tanaceteum vulgare L.
Taraxacum officionale Weber
Tragopogon dubius Scop.

Cornaceae
Cornus canadensis L.
Cornus stolonifera Michx.

Crassulaceae
Sedum stenopetalum Pursh.

Cruciferae
Arabas holboeli Hornem.
Cardamine breweri Wats.
Cardamine oligosperma Nutt.
Rorippa islandica (Oed.) Borbas
Rorippa nasturtium-aquaticum (d). S. & T.
Rorippa sinuata (Nutt.) A.S. Hitchc.
Sisymbrium loeslii L.
Thlaspi fendleri Gray, P.L. Wright var. glaucum (A. Nels.)

Cyperaceae
Carex athrostachya Olney
Carex bebbii Olney

TABLE 10 (CONTINUED)

Carex deweyana Schw.
Carex festivella Mack.
Carex geyeri Boott.
Carex hassei L.H. Bailey
Carex kelloggi W. Boott.
Carex lanuginosa Michx.
Carex leptopoda Mack.
Carex nebraskensis Dewey
Carex retrorsa Schw.
Carex rossii Boott.
Carex rostrata Stokes.
Carex saximontana Mack.
Carex stipata Muhl.
Carex vesicaria L.
Carex veridula Mich.
Carex sp.
Eleocharis machrostachya Britt.
Scirpus fimbrystylis

Eleagnaceae
Eleagnus comutata Bernh.
Shepherdia argentea (Pursh.) Nutt.
Shepherdia canadensis (L.) Nutt.

Equisetaceae
Equisetum arvense L.
Equisetum lavaegatum Br.

Ericaceae
Arctostaphylos uva-ursi (L.) Spreng.
Chimophila umbellata (L.) Bart.
Menziesia feruginea Smith var. glabella (Gray) Peck

Euphorbiaceae
Euphorbia esula L.

Geraniaceae
Geranium viscosissimum Fish and Mey.

Graminae
Agropyron inerme Heller
Agropyron repens (L.) Beauv.
Agropyron smithii Rydb.
Agropyron spicatum (Persh.) Scribn. and Smith.
Agrostis alba L.
Agrostis sp.
Agrostis tenuis Sibth.
Bromus inermus Leyss.
Bromus marginatus Nees.
Bromus tectorum L.
Calamagrostis canadensis(Michx.) Beauv.

TABLE 10 (CONTINUED)

Calamagrostis inexpansa Gray.
Dactylis glomerata L.
Danthonia intermedia Vasey.
Deschampsia caespitosa (L.) Beauv.
Elymus canadensis L.
Elymus glaucus Buckl.
Festuca occidentalis Hook.
Festuca idahoensis Elmer
Festuca rubra L.
Glyceria elata (Nash.) Hitchc.
Koeleria cristata (L.) Pers.
Muhlenburgia richardsonis (Trin.) Rydb.
Melica subulata (Griseb.) Scribn.
Phalaris arundinaceae L.
Phleum pratense L.
Poa compressa L.
Poa palustris L.
Poa pratensis L.
Poa trivialis L.
Poa sp.
Stipa columbiana Macoun.
Tirsetum cernuum Trin.
Triticum sp.

Grossulariaceae
Ribes americanum Mill.
Ribes hudsonianum Richards var. petiolare (Dougl.)
Ribes lacustre (Pers.) Poir.
Ribes setosum Lindl.

Hippocastanaceae
Aesculus Hippocastanum L.

Iridaceae
Iris missouriensis Nutt.
Sisyrenchium saramentosum Suksd.

Juncaceae
Juncus balticus Willd. var. montanus Engelm.
Juncus confusus Cov.
Juncus ensifolius Wikstr.
Juncus longistylis Torr.
Juncus nodosus L.
Juncus tenuis Wild. var. Dudleyi (Wieg) Hermann
Luzula multiflora (Retz.) Lejeune

Labiatae
Dracocephalum nuttallii Britt.
Gleocoma hederacea L.
Mentha arvensis L.

TABLE 10 (CONTINUED)

Monardna fistulosa L.
Napeta cataria L.
Prunella vulgaris L.
Scutellaria galericulata L.

Leguminosae
Astragalus sp.
Glycerhiza lepidota Pursh. var. lepidota
Hedysarum sulphurescens Rydb.
Lupinus sp.
Melilotus officionalis (L.) Lam.
Trifolium latifolium (Hook.) Greene
Trifolium longipes Nutt.
Trifolium pratense L.
Trifolium repens L.
Vicia americana Muhl. cx. Willd. var. truncata (Nutt.) Brent.

Lilliaceae
Allium cernuum Roth.
Allium schoenoprasum L.
Asparagus officionalis L.
Brodiaea Douglasii S. Wats.
Clintonia uniflora (Schult.) Kunth.
Disporum trachycarpum (S. Wats.) B.& H.
Erythronium grandiflorum Pursh.
Smilacina racemose (L.) Desf.
Smilacina stellata (L.) Desf.
Trillium ovatum Pursh.

Monotropaceae
Pterospora andromedea Nutt.

Onagraceae
Circaea alpine L.
Epibolium angustifolium L.

Ophioglossaceae
Botrychium virginianum (L.) SW.

Orchidaceae
Corallorhiza maculata Raf.
Goodyera sp.

Pinaceae
Abies grandis Lindl.
Juniperus communis L. var. montana Ait.
Juniperus scopulorum Sarg.
Larix occidentalis Nutt.
Picea engelmanni (Parry.) Engelm.
Pinus contorta Dougl. var. Murrayana Engel.
Pinus ponderosa Dougl.

TABLE 10 (CONTINUED)

Pseudotsuga menziesii (Mirb.) Franco
Thuja plicata D. Don
Tsuga heterophylla (Raf.) Sarg.

Plantaginaceae
Plantago major L.

Polemoniaceae
Microsteris gracilis (Dougl. ex. Hook.) Greene
Polemonium occidentalis Greene

Polygonaceae
Polyganum natans (Michx.) Eaton
Rumex acetosella L.
Rumex crispus L.
Rumex meritimus L.
Rumex sp.

Polypodiaceae
Aytherium felix-foemina (L.) Roth.
Dryopteris cristata (L.) A. Gray
Polypodium hesperium Maxon
Pteridium aquilinum var. languinosum (Bong.) Fernald

Portulacaceae
Claytonia perfoliata Donn.
Montia cordifolia (Wats.) Pax & K. Hoffm. in E. & P.

Primulaceae
Steironema ciliata (L.) Raf.

Pyrolaceae
Chimaphila umbellata (L.) Bart. var. occidentalis (Rydb.) Blake.
Pyrola asarifolia Michx.
Pyrola secunda L.
Pyrola virens Schweigg.

Ranunculaceae
Actaea rubra (Ait.) Willd.
Anemone multifida Poir.
Anemone parviflora Michx.
Clematis columbiana (Nutt.) T. & G.
Clematis lingusticifolia Nutt.
Ranunculus abortivus L.
Ranunculus uncinatus D.
Thallictrum venulosum Trel.

Rhamnacea
Rhamnus alnifolia L' Her.

TABLE 10 (CONTINUED)

Rosaceae
Amelanchier alnifolia Nutt.
Crataegus douglasii Lindl.
Dryas drummondii Richards ex. Hook.
Fragaria virginiana Duchesne var. ovalis (Lehm.) Davis.
Geum macrophyllum Willd. var. macrophyllum
Holodiscus discolor (Pursh.) Maxim.
Physocarpus malvaceus (Greene) Kuntze.
Potentilla arguta Pursh.
Potentilla fruiticosa L.
Prunus virginiana L. var demissa (Nutt.) Torr.
Rosa gymnocarpa Nutt.
Rosa woodsii Lindl.
Rosa acicularis Lindl.
Rubus idaeus L.
Rubus parviflorus Nutt.
Sorbus scopulina Greene
Spiraea betulifolia Pall.

Rubiaceae
Galium aparine L. var. echinospermum (Wallr.) Farwell.
Galium boreale L.
Galium trifidium L.
Galium triflorum Michx.

Salicaceane
Populus tremuloides Michx.
Populus trichocarpa T. & G. ex. Hook.
Salix alba L.
Salix bebbiana Sarg.
Salix exigua Nuttall
Salix sp.

Saxifragaceae
Boykenia major Gray var. major
Castelleja sp.
Lithophragma parviflora (Hook.) Nutt. ex. T. & G.
Mitella stauropetala Piper.
Philadelphus lewisii Pursh.
Tiarella unifoliata Nutt.

Scrophulariaceae
Collinsia parviflora Lindl.
Linaria vulgaris Hill.
Mimusus guttatus D.C.
Mimulus moschatus Dougl. in Lindl.
Penstemon albertinus Greene
Penstemon procerus Dougl. ex. R. Grah. Edinb. var. procerus
Verbascum thapse L.

TABLE 10 (CONTINUED)

Solanaceae
    Solanum dulcamara L.

Umbelliferae
    Angelica arguta Nutt.
    Heracleum lantanum Michx.
    Osmorhiza chilensis H. & A.
    Osmorhiza occidentalis (Nutt.) Torr.
    Sium suave Watt.

Urticaceae
    Urtica dioica L.

Violaceae
    Viola adunca Sm.
    Viola glabella Nutt.
    Viola orbiculata Geyer. er. Hook.
    Viola rugulosa Greene

TABLE 11. THE ARRANGEMENT OF BOTTOMLAND FOREST STANDS ACCORDING TO TREE DIAMETER SIZE

Stand No.	Location	Tree Size Distribution 4-10*	11-20	21-30	30+	Quartile
44	t	15	28	24	13	
3	t	44	7	15	14	
4	t	35	21	14	10	IV
2	t	34	29	15	2	
15	f	45	21	11	3	
23	t	49	19	8	4	
1	t	43	25	10	2	
24	f	39	31	9	1	
9	f	26	47	7	0	
20	f	44	32	2	2	III
13	f	26	51	3	0	
22	f	35	43	2	0	
6	t	52	27	0	0	
10	f	56	23	1	0	
7	f	57	23	0	0	
16	f	60	20	0	0	
8	f	62	18	0	0	II
18	ox	64	15	1	0	
14	f	65	15	0	0	
21	f	74	6	0	0	
5	f	74	5	1	0	
12	f	74	6	0	0	I
19	ox	78	2	0	0	

*Tree sizes are in inch units.

TABLE 12. LIST OF SPECIES USED IN THE "TREE" ORDINATION

Trees and Saplings*	Abies grandis Acer glabrum Alnus incana Betula occidentalis Crataegus douglasii Juniperus scopulorum Larix occidentalis Picea engelmanni Pinus contorta Pinus ponderosa Populus tremuloides Populus trichocarpa Prunus virginiana Pseudotsuga menziesii Pyrus sp. Salix alba Thuja plicata Tsuga heterophylla
Herbs and Seedlings	Acer glabrum Agropyron repens Circaea alpina Elymus glaucus Galium triflorum Osmorhiza chilensis Prunus virginiana Rosa woodsii Smilacina stellata Symphoricarpos albus

TABLE 13. HERBACEOUS PLANTS USED IN THE "UNDERSTORY" ORDINATION

Acer glabrum
Achillea millefolium
Agropyron inerme
Agropyron repens
Amelanchier alnifolia
Angelica arguta
Atherium felix-foemina
Berberis repens
Betula occidentalis
Bromus inermus
Bromus sp.
Calamagrostis canadensis
Centaurea maculosa
Chrysopsis villosa
Circaea alpina
Cirsium arvense
Clematis columbiana
Cornus stolonifera
Crataegus douglasii
Disporum trachycarpum
Eleagnus comutata
Elymus glaucus
Epilobium angustifolium
Equisetum fluviatile
Equisetum arvense
Fragaria virginiana
Galium trifidium
Geum macrophyllum
Glycerhiza lepidota
Hieracium albiflorum
Juniperus communis
Mentha arvensis
Osmorhiza chilensis
Phleum pratense
Poa compressa
Poa palustris
Poa pratensis
Poa sp.
Polypodium hesperium
Populus tremuloides
Populus trichocarpa
Prunella vulgaris
Pyrola asarifolia
Ranunculus abortivus
Rosa woodsii
Rubus idaeus
Rubus parviflorus
Shepherdia argentea
Smilacina stellata
Solanum dulcamara
Symphoricarpus albus
Tanacetum vulgare
Taraxacum officionale
Thallictrum venulosum
Trifolium pratense
Trifolium repens
Urtica dioica
Vicia americana
Viola sp.

TABLE 14. HERBS, SHRUBS, AND SEEDLINGS COMMON TO THE TRIBUTARY STANDS

Species	Occurrences in tributaries	Occurrences in floodplains	Occurrences in higher elevation
Heracleum lantanum	6	1	1
Osmorhiza chilensis	7	0	0
Urtica dioica	6	1	0
Thallictrum venulosum	7	2	3
Disporum trachycarpum	7	1	0
Actea rubra	6	0	2
Circaea alpina	5	0	0
Tricetum dernuum	3	1	0
Carex leptopoda	4	0	0
Polypodium hesperium	4	0	0
Mitella stauropetala	3	0	0
Carex saximontana	2	0	0
Berberis repens	6	0	2
Pyrola asarifolia	6	0	2
Cerastium vulgatum	4	2	0
Petasites sagittata	1	0	0
Senecio triangularis	3	1	0
Glyceria elata	3	0	0
Luzula multiflora	2	0	0
Napeta cataria	1	0	0
Aytherium felix-foemina	5	0	0
Pteridium aquilinum	2	0	0

TABLE 14 (CONTINUED)

Species	Occurrences in tributaries	Occurrences in floodplains	Occurrences in higher elevation
Montia cordifolia	2	0	0
Angelica arguta	4	1	1
Smilacina racemosa	4	0	0
<u>Shrubs</u>			
Ribes setosum	4	1	0
Philadelphus lewisii	5	1	0
Spireae betulifolia	3	0	0
Sorbus scopulina	4	0	0
Rubus parviflora	4	1	2
Rubus idaeus	7	1	2
Holodiscus discolor	4	0	0
Amelanchier alnifolia	7	4	2
Rhamnus alnifolia	2	0	1
Ribes hudsonianum var. petiolare	3	0	0
<u>Seedlings</u>			
Acer glabrum	6	0	0
Alnus incana	6	1	1
Betula occidentalis	6	1	1
Abies grandis	1	0	0
Pseudotsuga menziesii	3	1	2
Populus tremuloides	3	0	1

TABLE 15. HERBS, SHRUBS AND SEEDLINGS COMMON TO THE FLOODPLAIN STANDS

Species	Occurrences in tributaries	Occurrences in floodplains	Occurrences in higher elevation
Agropyron repens	0	6	0
Bromus inermus	3	5	3
Poa compressa	1	5	0
Juncus balticus	0	2	2
Calamagrostis canadensis	3	5	3
Glycerhiza lepidota	0	3	2
Tanacetum vulgare	0	7	0
Poa pratensis	3	6	1
Rumex crispus	0	4	0
Poa palustris	2	6	1
Solidago canadensis	2	4	0
Silene cucabalis	0	2	0
Artemesia lendeyana	0	2	0
Centaurea maculosa	3	6	0
Chrysanthemum leucanthemum	0	3	2
Chrysopsis villosa	0	3	2
Aster laevis	1	4	0
Senecio canus	0	1	1
Trigopogoa dubium	0	4	2
Arabis holboelii	0	2	0
Asparagus officionale	0	4	0
Vicia americana	2	3	1
<u>Seedlings</u>			
Populus trichocarpa	7*	6	4
Juniperus scopulorum	0	1	0
Pinus ponderosa	5*	4	2

*Although these species are common to both the tributaries and the floodplains, they reach their highest frequencies in the floodplains.

TABLE 16. HERBS, SHRUBS, AND SEEDLINGS COMMON TO THE HIGHER ELEVATION STANDS

Species	Occurrences in tributaries	Occurrences in floodplains	Occurrences in higher elevations
Aster foliaceus	0	0	4
Aster hesperius	0	0	1
Erigeron specious	0	0	2
Gaillardia aristata	0	3	3
Prenanthes sagittata	0	0	2
Senecio pauperculus	0	0	2
Solidago missouriensis	0	1	4
Carex hassei	0	0	2
Carex veridula	0	0	1
Deschampsia caespitosa	0	1	3
Koeleria cristata	0	0	3
Stipa columbia	0	0	2
Bromus marginatus	0	0	1
Sisyrenchium sarmentosum	0	0	2
Hedysarum sulphurescens	0	0	1
Allium cernuum	0	1	2
Allium schoenoprasum	0	0	4
Anemone multifida	0	0	1
Dryas drummondii	0	1	3
Antennaria rosea	0	1	4
Shrubs			
Eleagnus comutata	0	0	2
Shepherdia argentea	0	0	4
Potentilla fruiticosa	0	1	3
Seedlings			
Juniperus communis	0	2	3
Pinus contorta	0	1	2
Picea engelmanni	1	0	2

TABLE 17. SOIL ANALYSIS SUMMARY FOR THE BOTTOMLAND FOREST STANDS

Stand No.	pH	P	K	Ca	Mg	NO_3	NH_3
1	6.7	85*	500	25,000	1,490	35	15
2	6.5	107	495	13,900	1,290	5	7
3	7.1	59	480	12,350	1,190	30	30
4	6.5	68	422	14,000	1,450	64	13
5	5.9	56	515	3,000	1,090	8	15
6	5.6	18	265	5,805	915	3	28
7	5.8	145	156	2,350	585	7	25
8	7.3	200	377	1,200	1,695	38	615
9	---	---	---	-----	-----	--	---
10	7.1	110	160	1,275	350	8	70
12	7.6	5	138	69,000	4,000	3	25
13	7.6	23	173	66,000	6,500	1	25
14	7.6	3	135	140,000	1,800	2	10
15	7.5	250	425	12,200	5,550	8	40
18	7.2	188	363	19,400	1,750	60	20
19	7.4	71	208	30,000	3,400	13	20
20	7.5	5	208	46,000	3,025	3	15
21	---	---	---	------	-----	--	--
22	6.4	275	298	5,550	3,650	T	10
23	6.3	295	328	5,050	640	T	15
24	5.9	200	183	2,450	495	5	13
44	---	---	---	-----	---	--	--

---- Indicates that samples were not analyzed
T Indicates that only a trace of the element was present.
* Units given in pounds per acre.

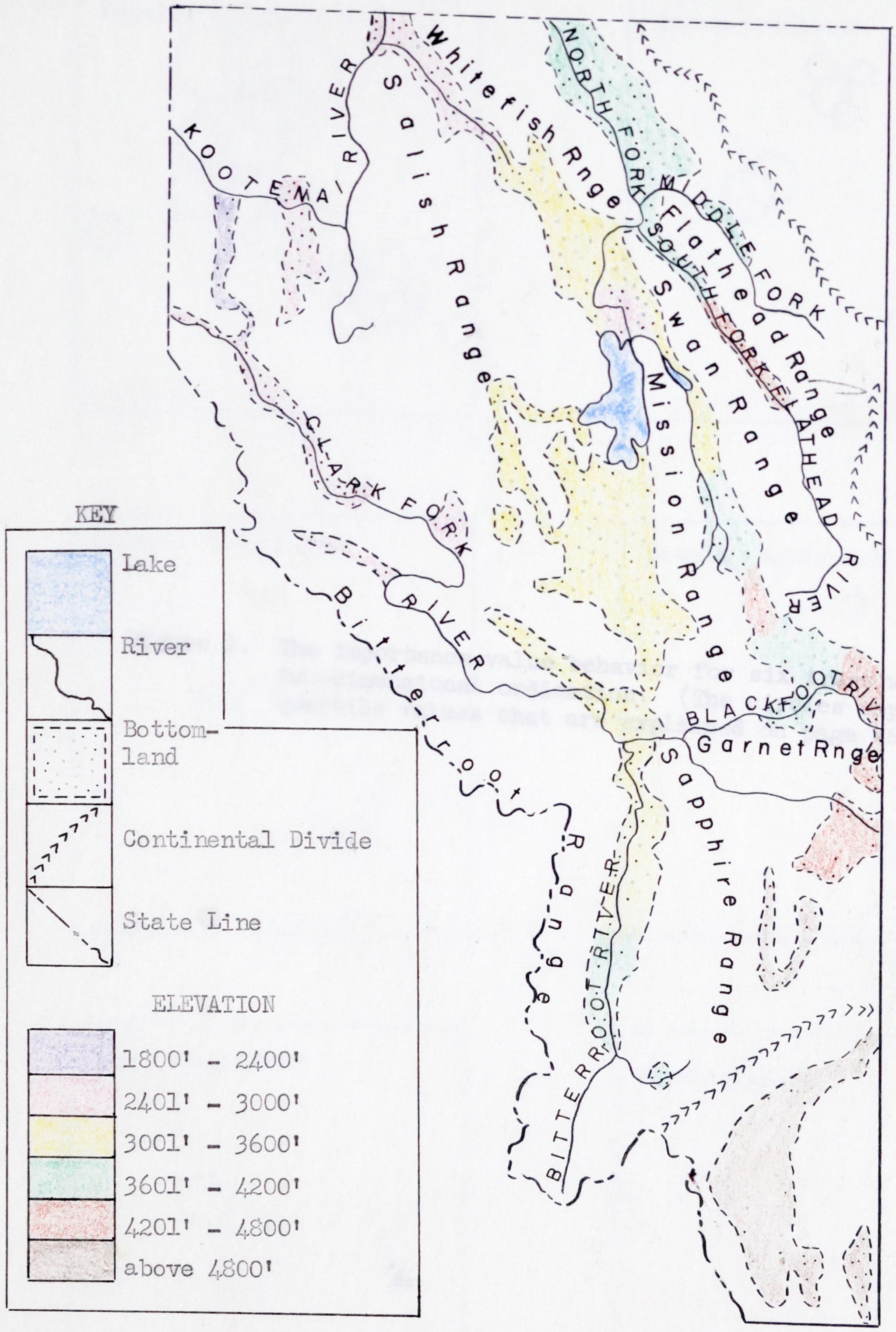
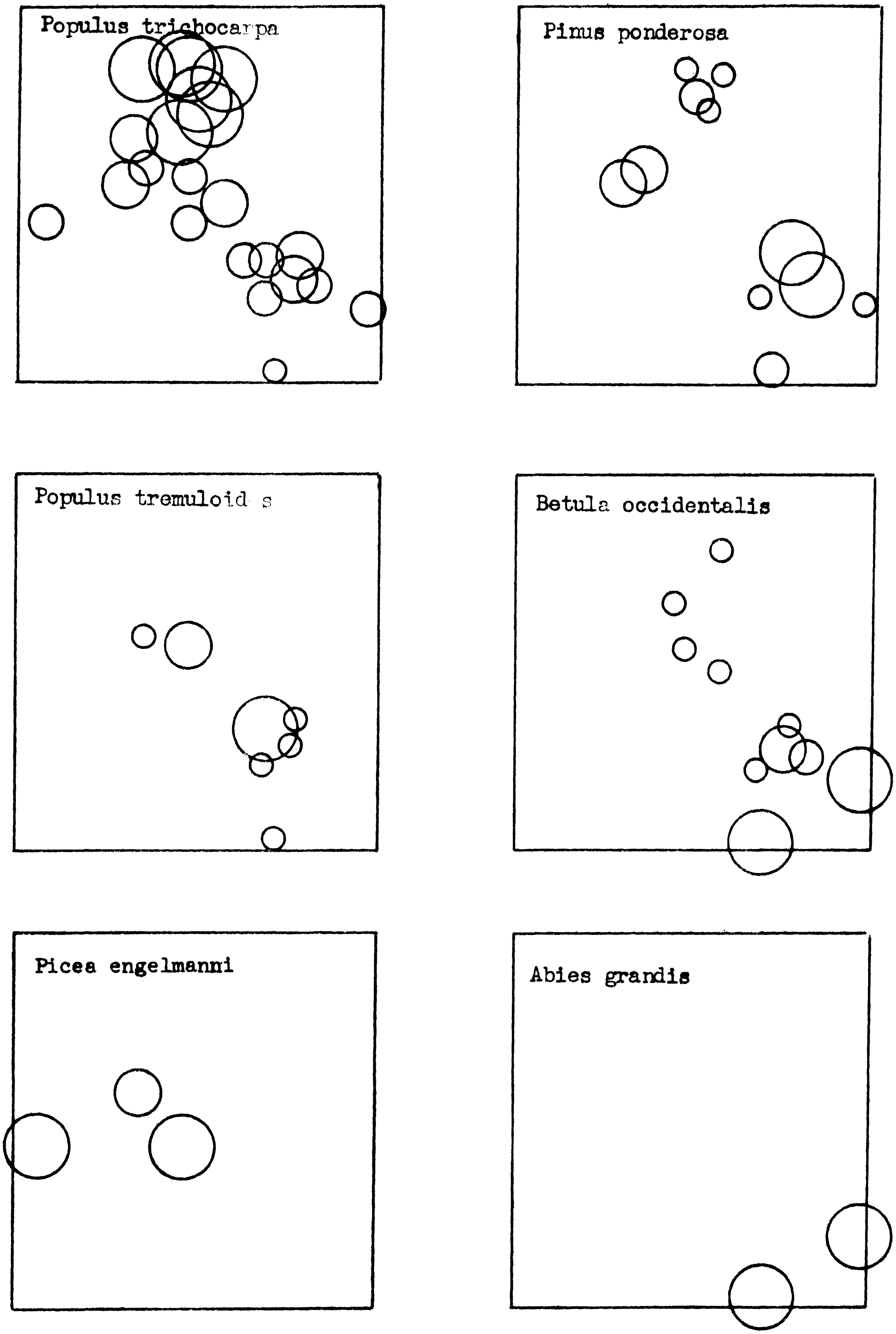


Figure 1. Map of study area showing bottomland stand locations and elevations.

Figure 2. The importance value behavior for six trees within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)


Populus trichocarpa
Pinus ponderosa
Populus tremuloides
Betula occidentalis
Picea engelmanni
Abies grandis

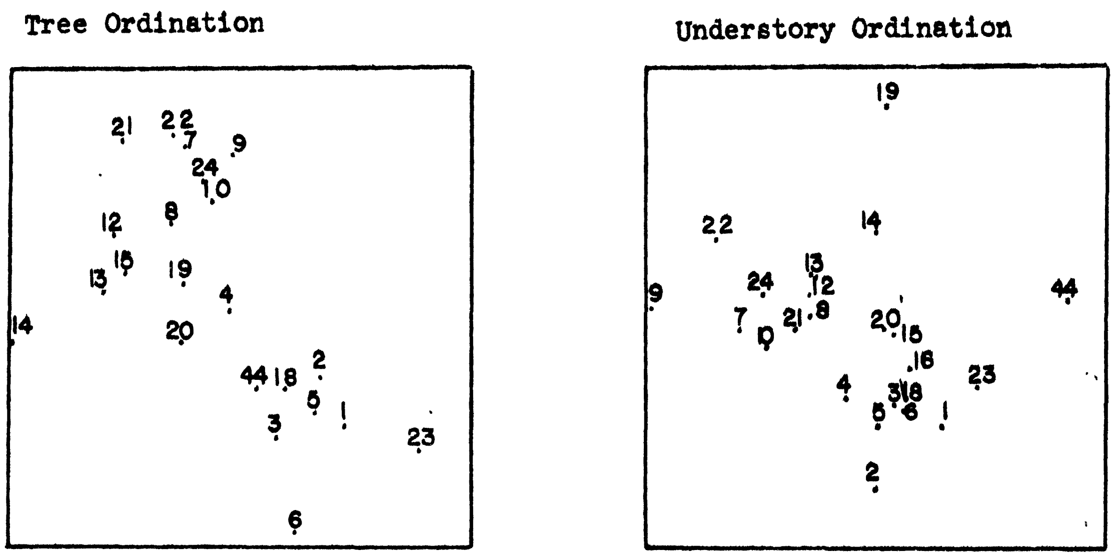
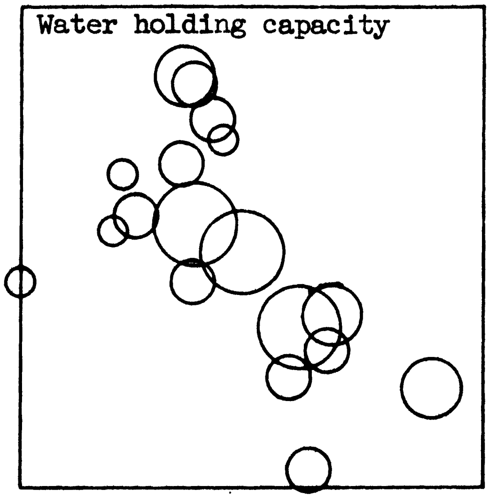


Figure 3. Distribution of stands in the two-dimensional "tree" and "understory" ordinations.

Figure 4. Behavior of soil water holding capacity and the organic matter within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)


Water holding capacity

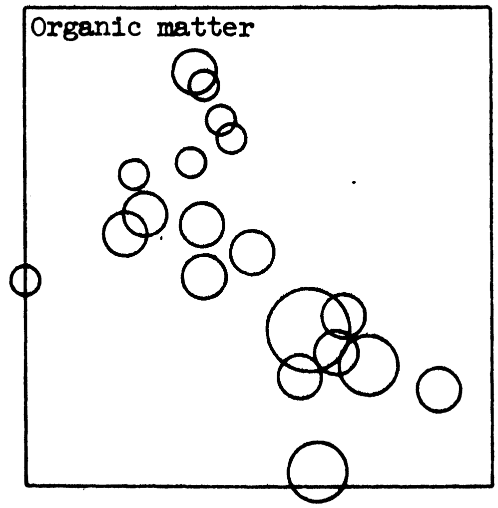

Organic matter

Figure 5. The importance value behavior for six trees within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

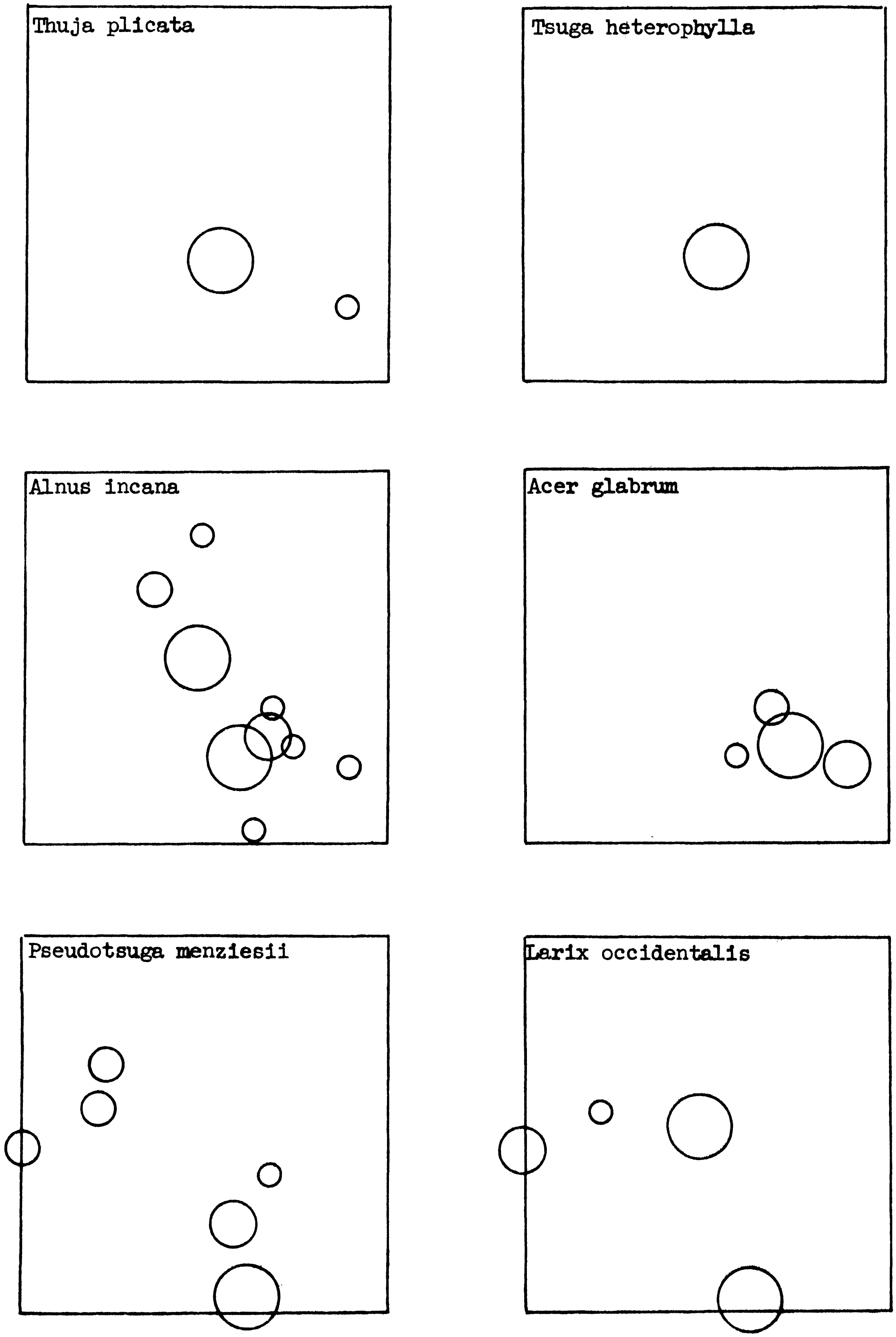

Thuja plicata
Tsuga heterophylla
Alnus incana
Acer glabrum
Pseudotsuga menziesii
Larix occidentalis

Figure 6. The behavior of total tree density and the tree density for five trees within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

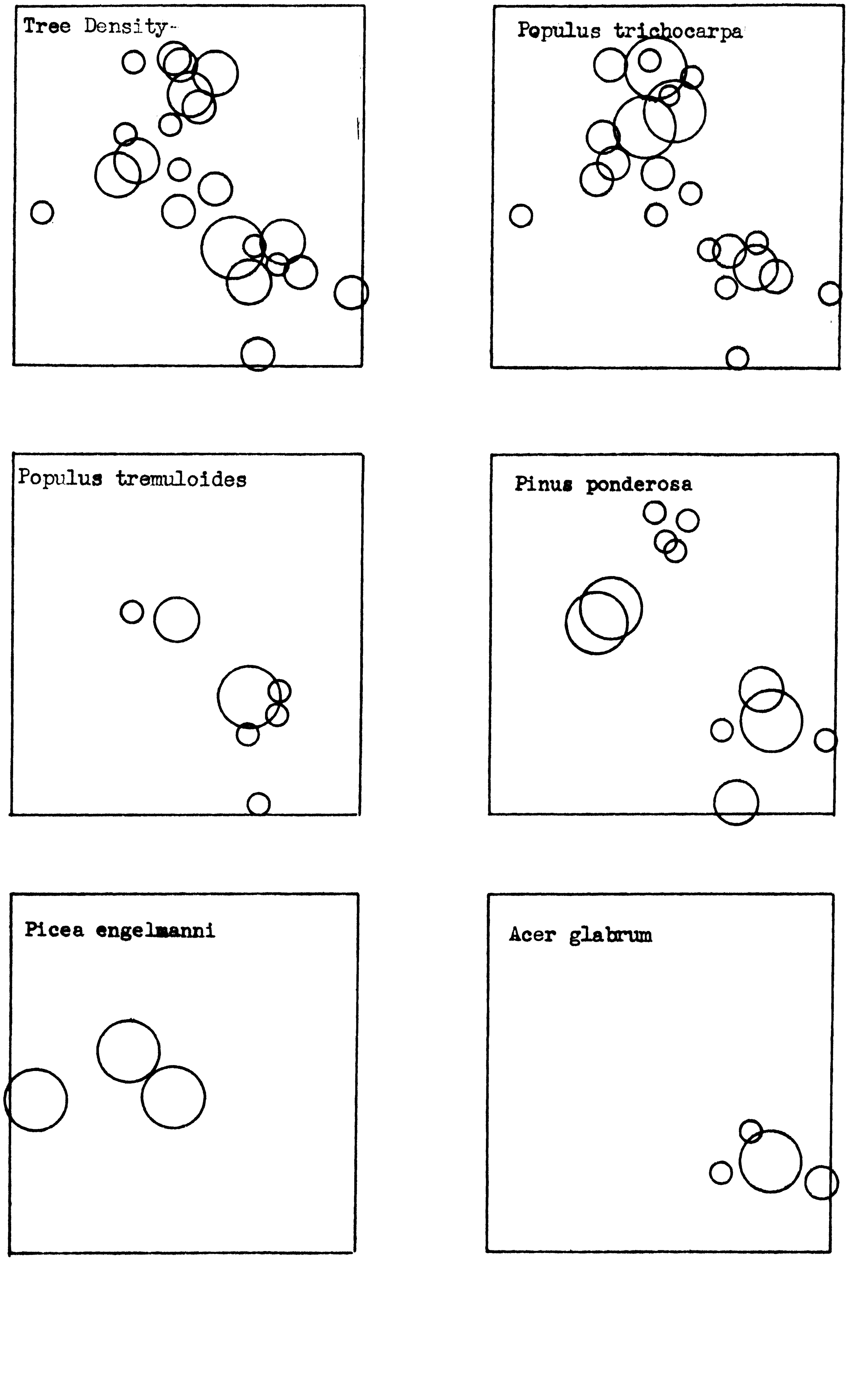

Tree Density
Populus trichocarpa
Populus tremuloides
Pinus ponderosa
Picea engelmanni
Acer glabrum

Figure 7. The behavior of total sapling density and sapling density for five trees within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

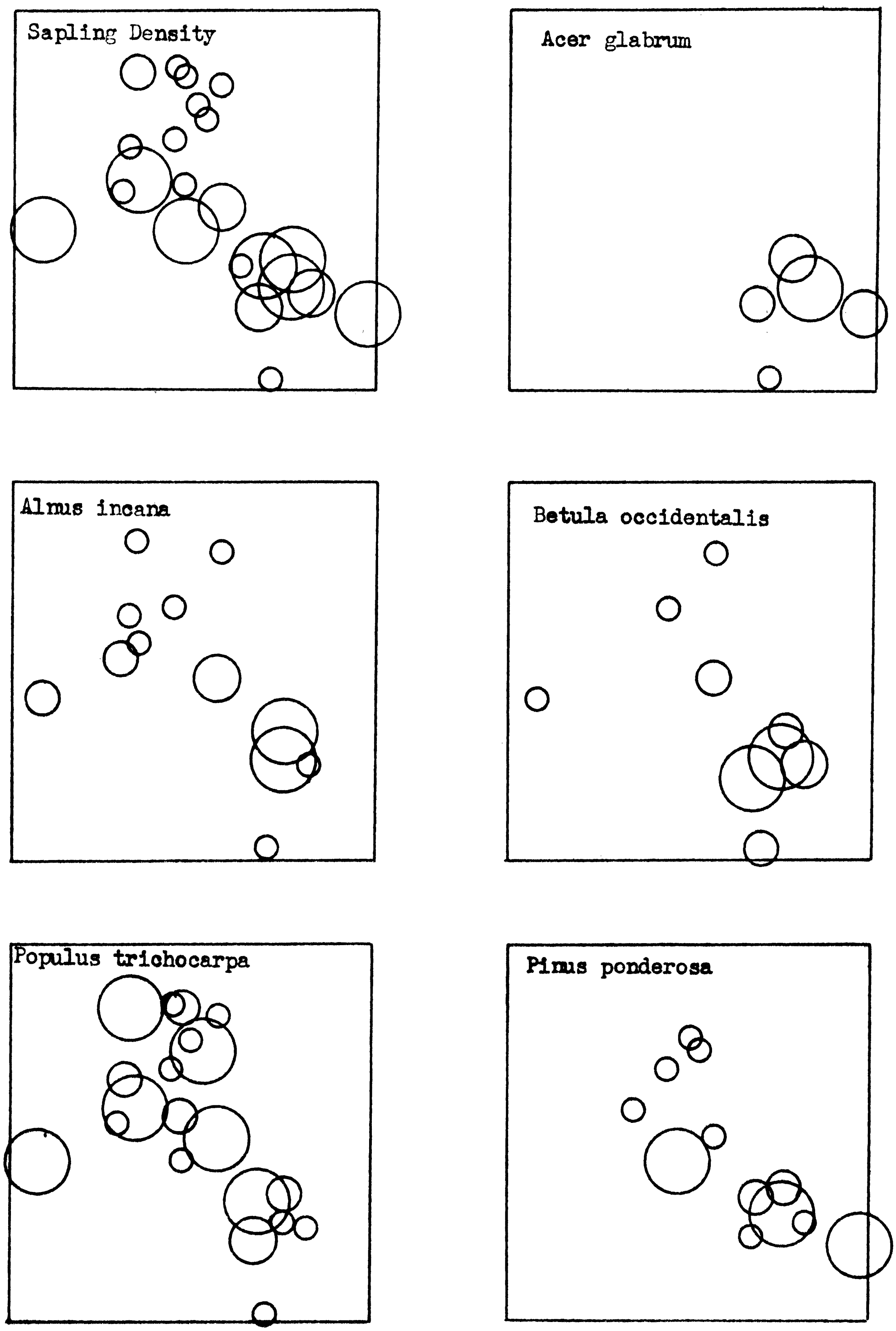

Sapling Density
Acer glabrum
Alnus incana
Betula occidentalis
Populus trichocarpa
Pinus ponderosa

Figure 8. The behavior of six saplings within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

* indicates IV quartile given arbitrarily (see page 56.)

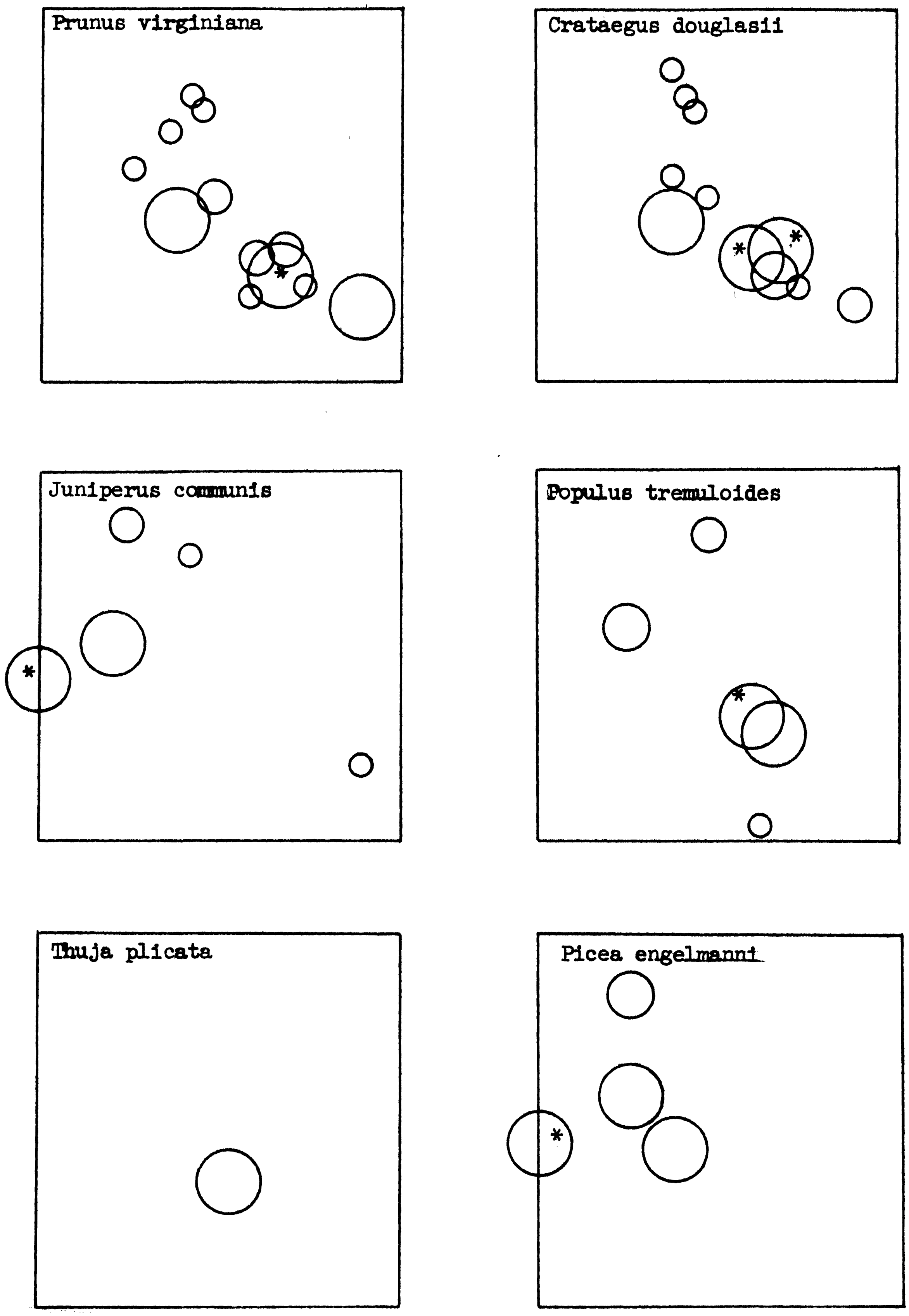
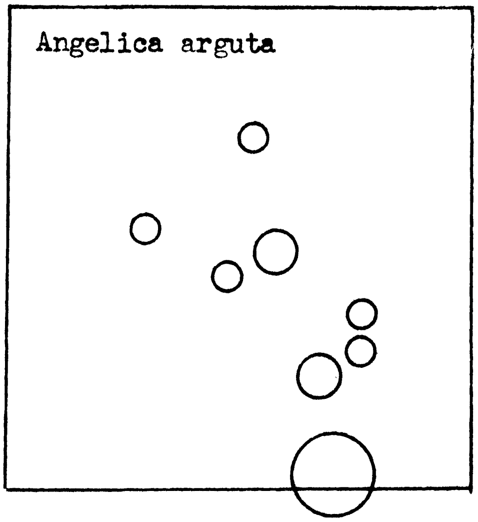
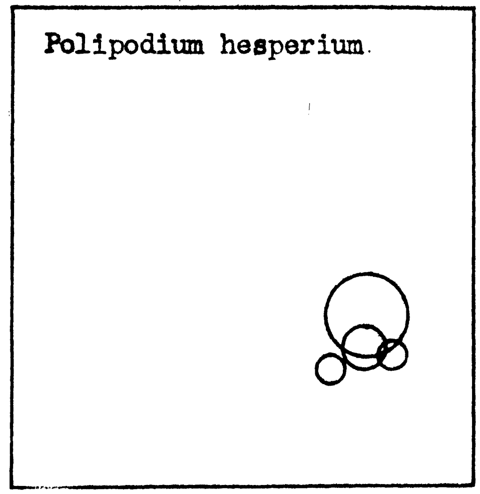
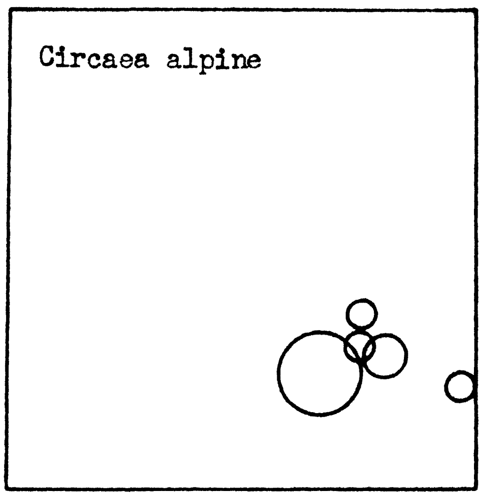
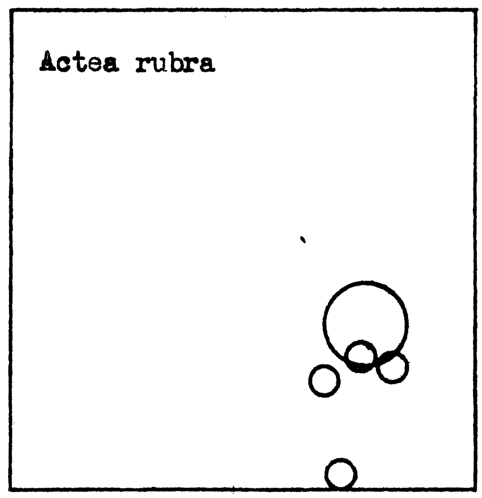

Prunus virginiana
Crataegus douglasii
Juniperus communis
Populus tremuloides
Thuja plicata
Picea engelmanni

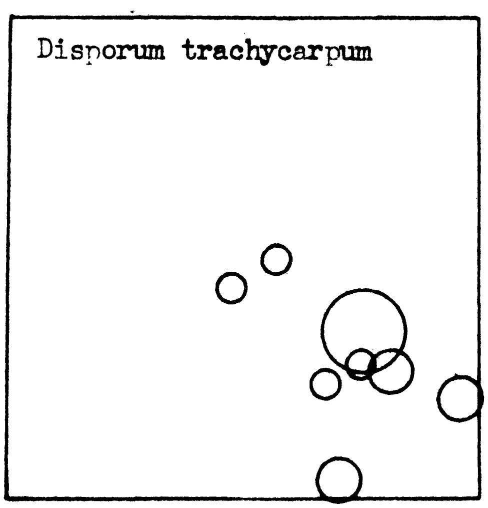
Figure 9. The behavior of six herbs most common to the tributary stands within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)


Angelica arguta


Polipodium hesperium


Circaea alpine


Actea rubra


Disporum trachycarpum

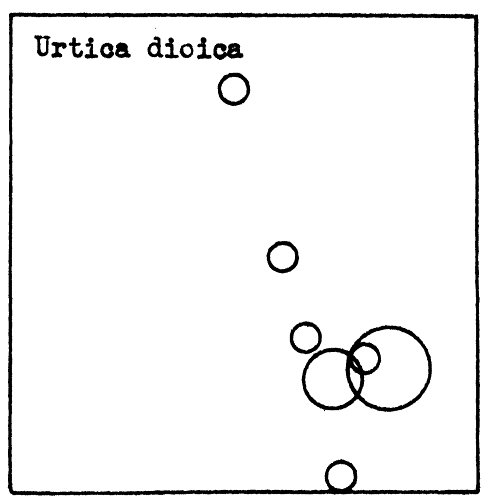

Urtica dioica

Figure 10. The behavior of six herbs most common to the tributary stands within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

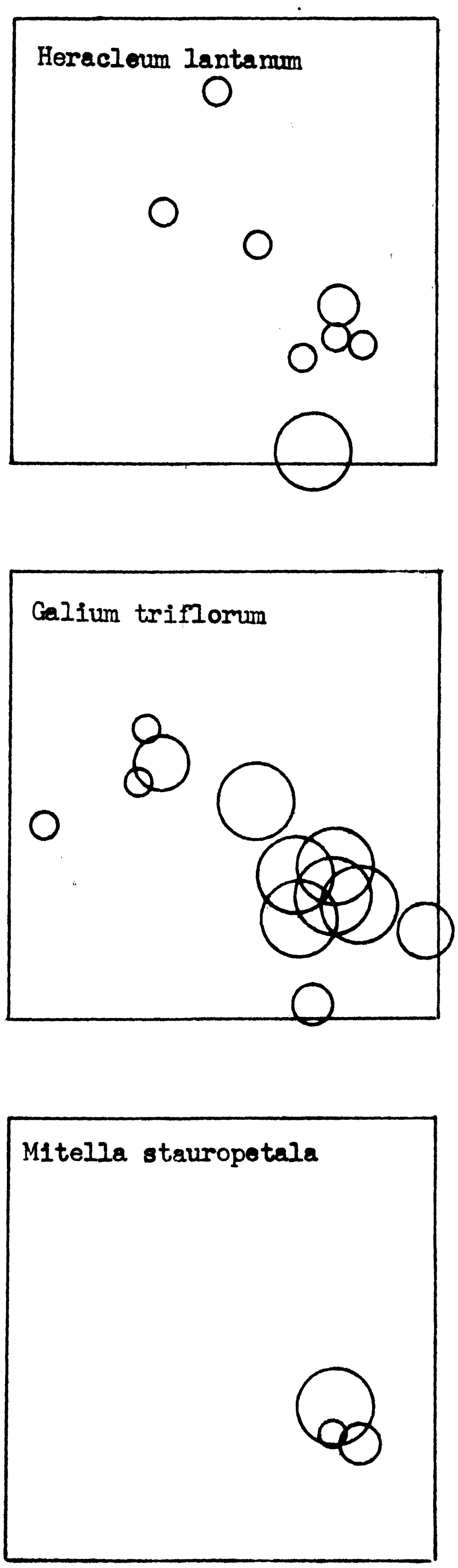

Heracleum lantamm
Osmorhiza chilensis
Galium triflorum
Pteridium aquilimm
Mitella stauropetala
Aytherium felix-foemina

Figure 11. The behavior of six shrubs within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

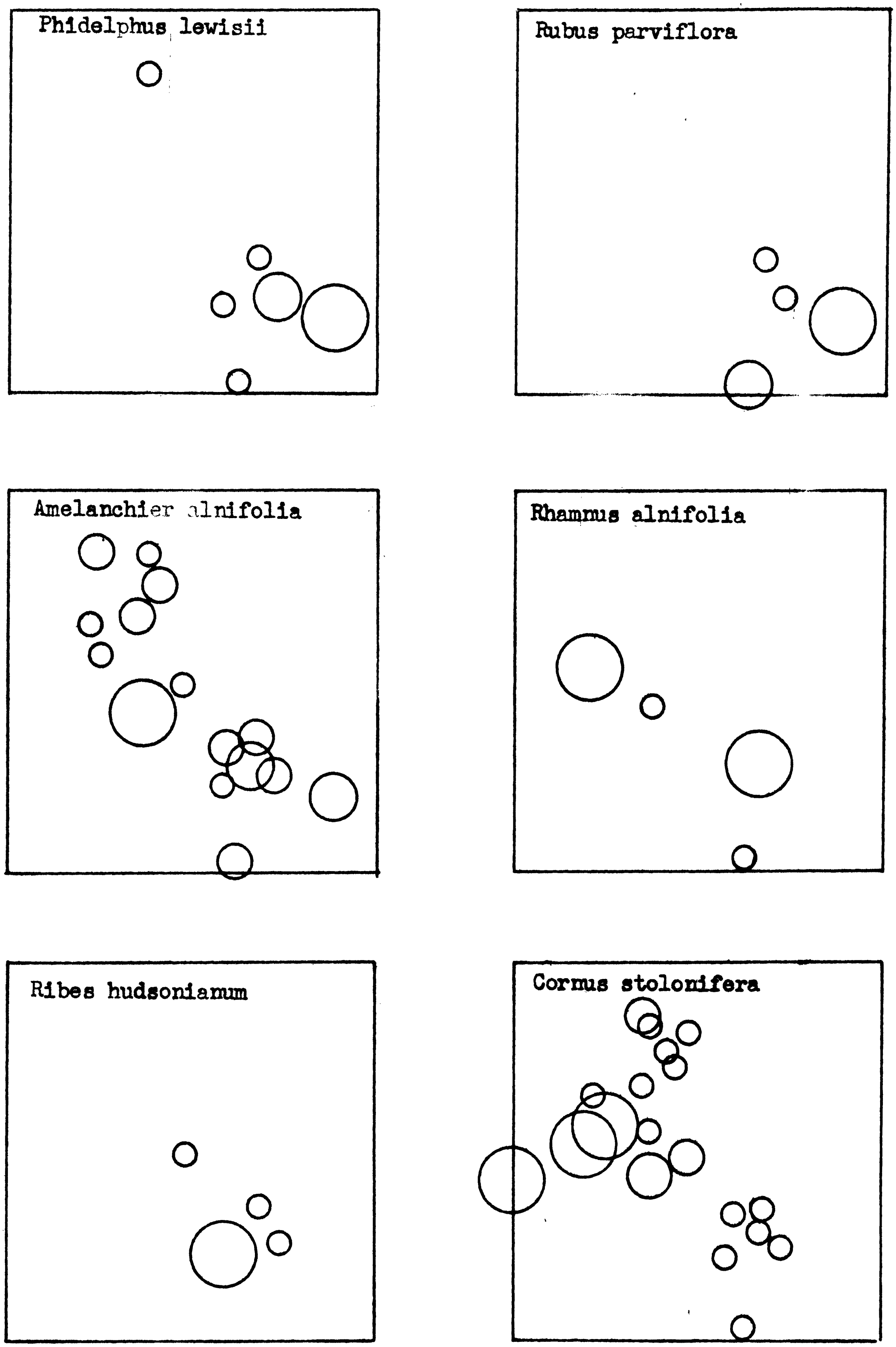

Phidelphus lewisii
Rubus parviflora
Amelanchier alnifolia
Rhamnus alnifolia
Ribes hudsoniamum
Cornus stolonifera

Figure 12. The behavior of six shrubs within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

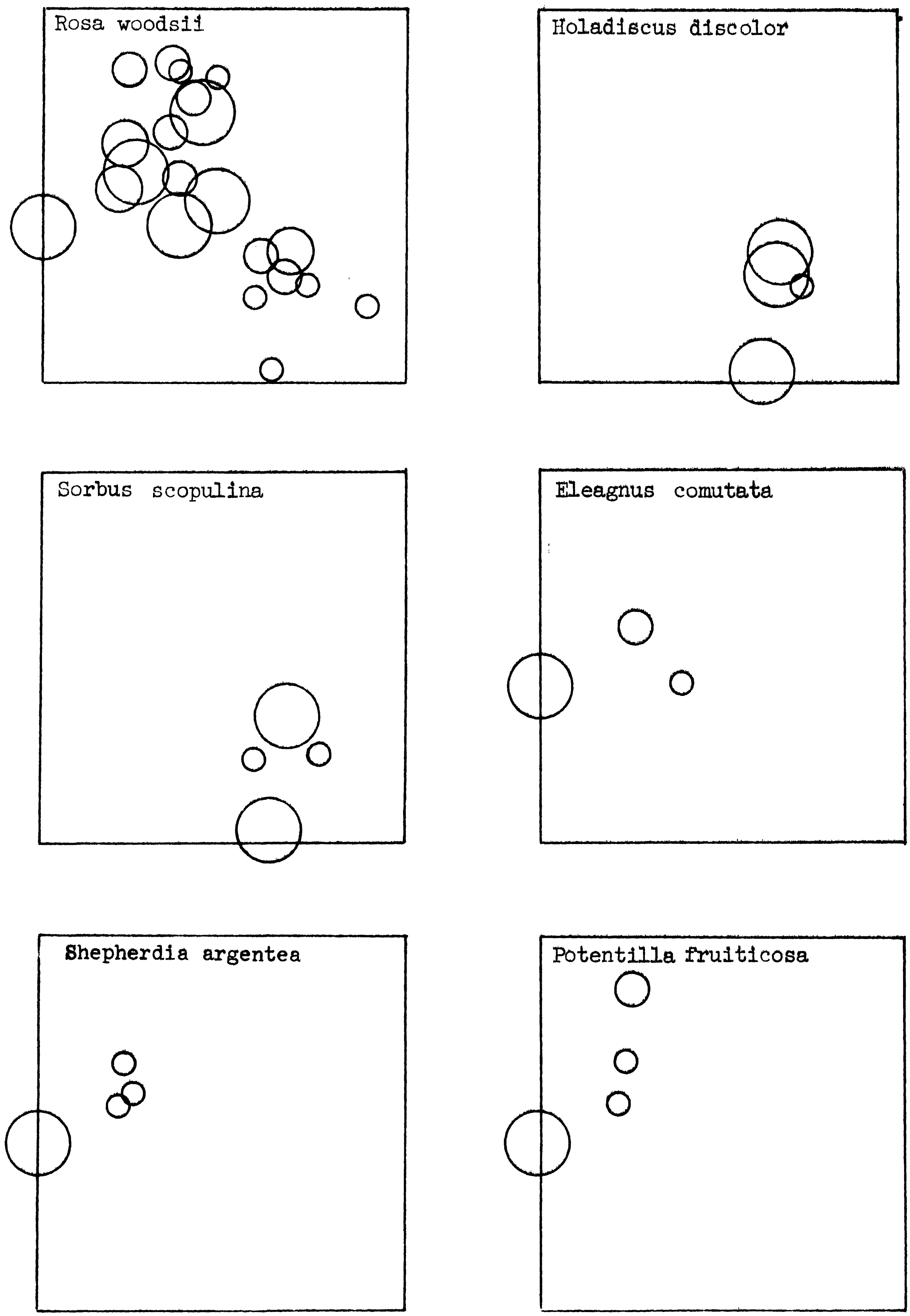
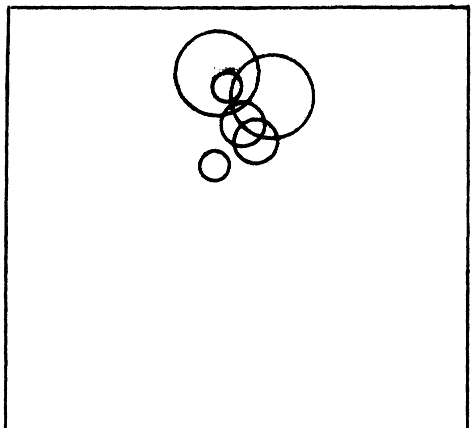
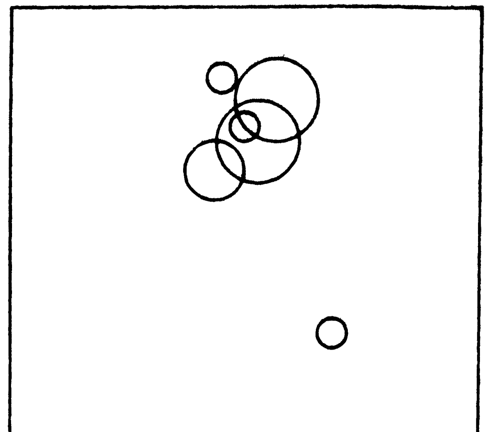

Rosa woodsii
Holadiscus discolor
Sorbus scopulina
Eleagnus comutata
Shepherdia argentea
Potentilla fruiticosa

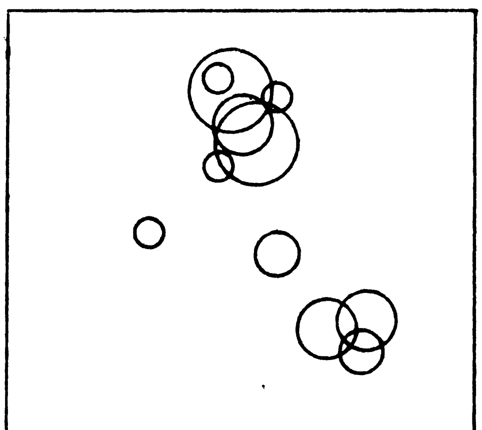
Figure 13. The behavior of six shrubs most common to the floodplains within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)



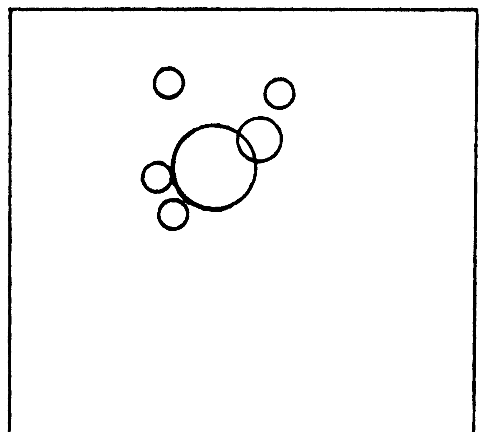
Agropyron repens



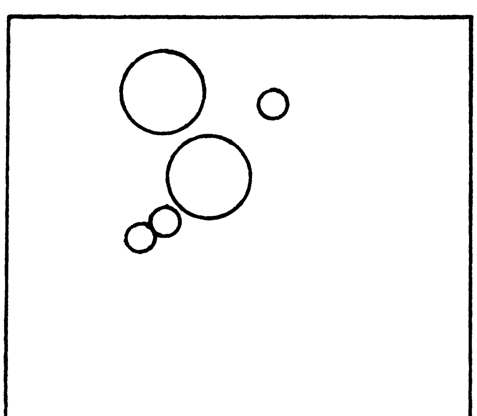
Poa compressa



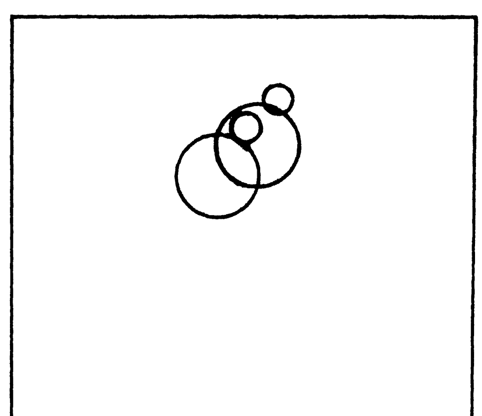
Poa pratensis



Trigopogon dubius

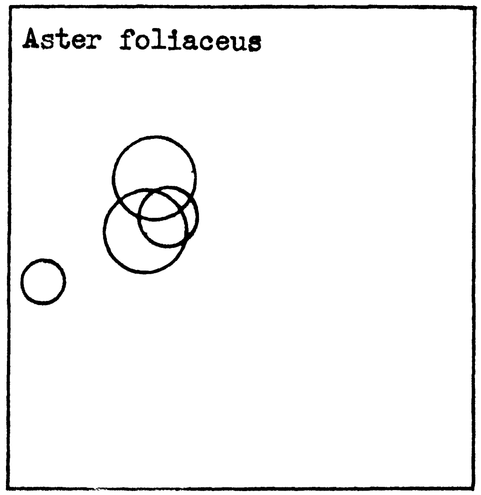


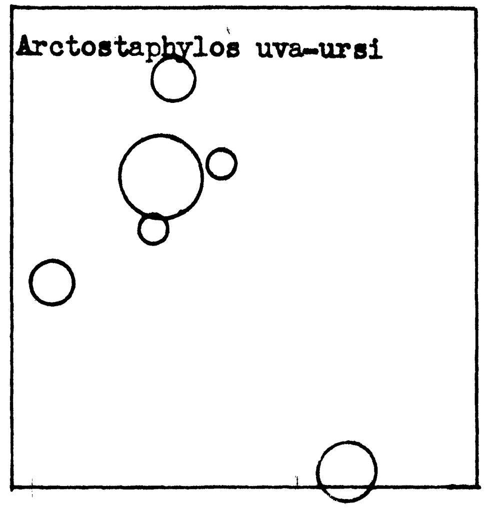
Chrysopsis villosa

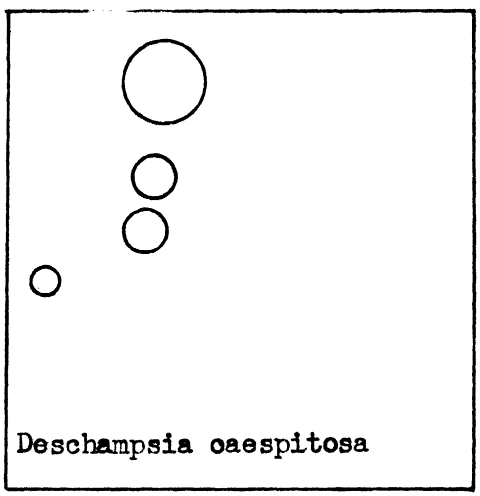


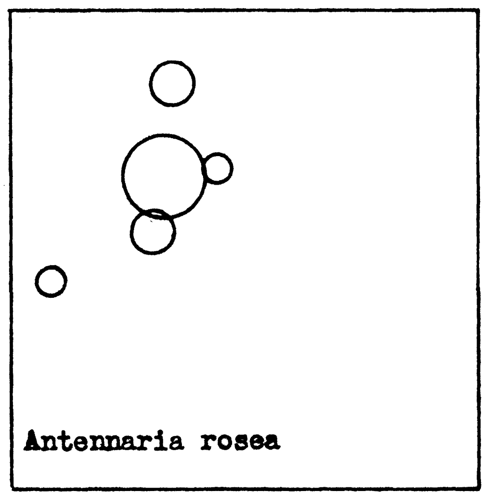
Asparagus officionale

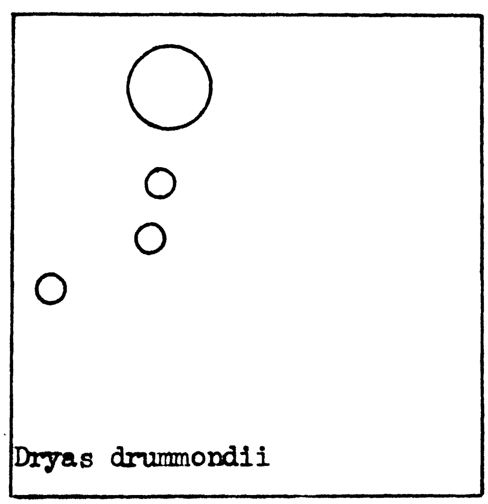
Figure 14. The behavior of six herbs most common to the higher elevational stands within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)


Aster foliaceus


Arctostaphylos uva-ursi


Deschampsia caespitosa


Antennaria rosea


Dryas drummondii

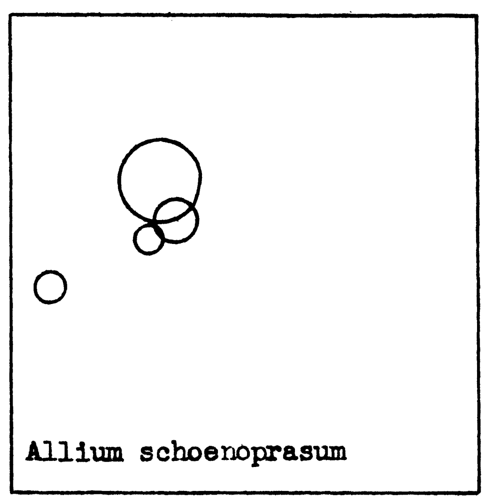
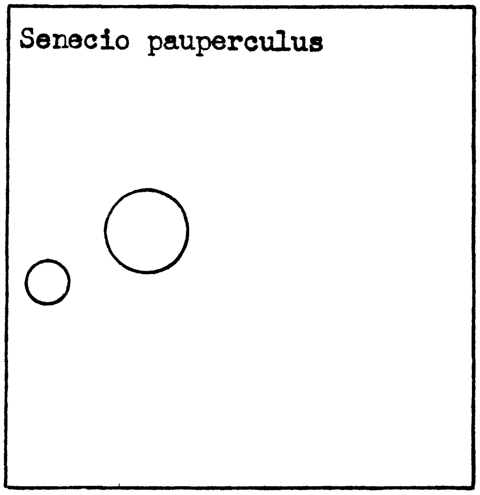
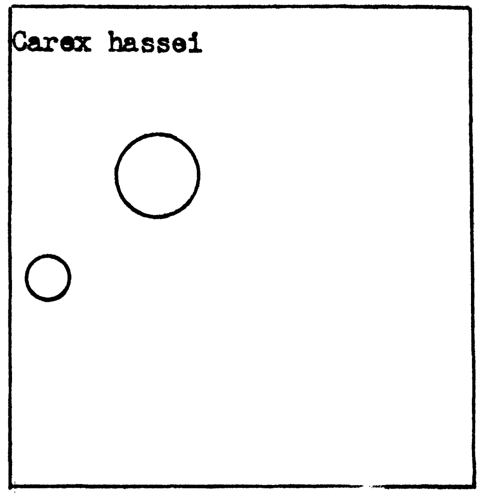
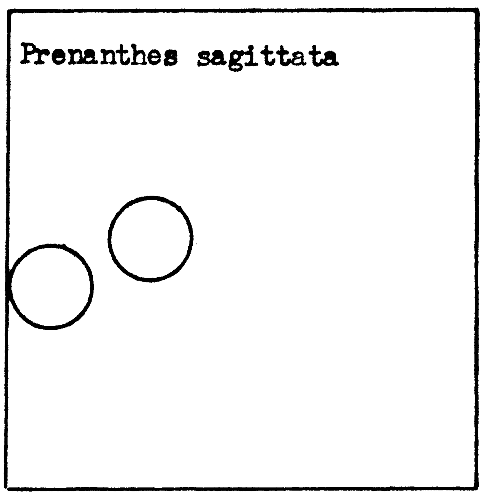
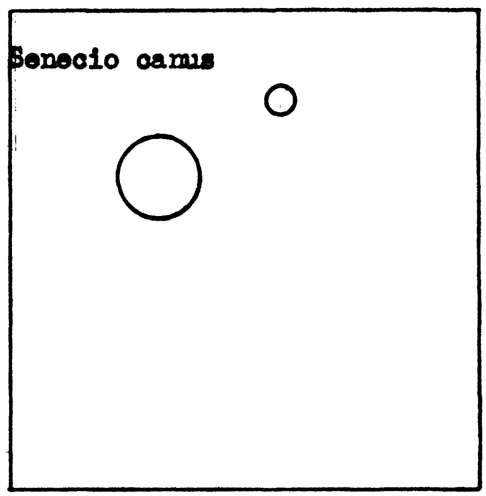

Allium schoenoprasum

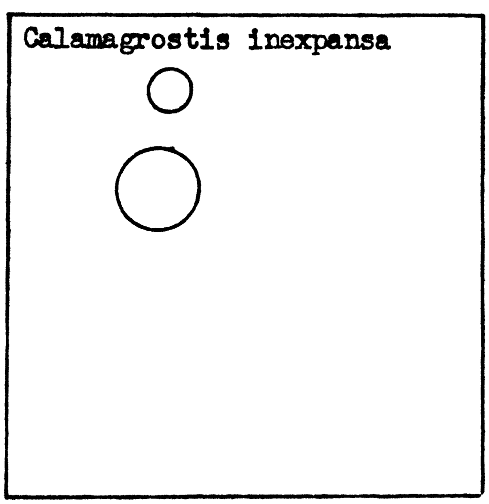
Figure 15. The behavior of six herbs most common to the higher elevational stands within the two-dimensional ordination. (The circles represent the quartile values that are explained on page 46.)

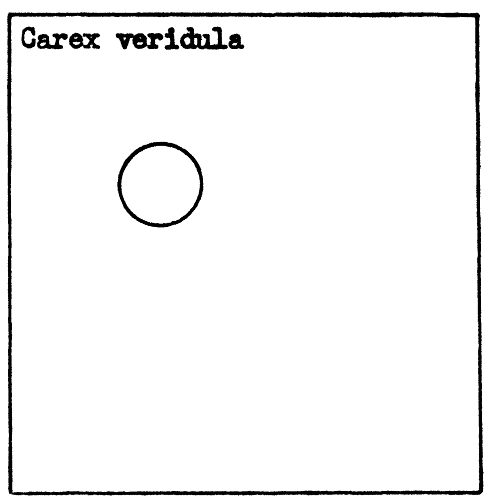

Senecio pauperculus


Carex hassei


Prenanthes sagittata


Senecio canus


Calamagrostis inexpansa


Carex veridula